

THE TAPHONOMY AND PALEOECOLOGY OF PLIO-PLEISTOCENE VERTEBRATE ASSEMBLAGES EAST OF LAKE RUDOLF, KENYA

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ABSTRACT. The object of this study is to show that paleoecologic information can be derived from fossil vertebrate assemblages fragmented prior to burial if a taphonomic history can be established for these assemblages. Such paleoecologic information can lead to knowledge of the character and evolution of vertebrate communities through time. Within the Koobi Fora Formation of East Rudolf, Kenya, vertebrate bones are preserved in fluvial and lacustrine depositional environments through a time span between about 3.0 and 1.2 million years Before Present. A total of seven bone assemblages were collected from lake margin, channel and floodplain deposits. Detailed geological studies were done in the seven laterally extensive sedimentary environments sampled for bones. The bone samples were taken from surface lag concentrations utilizing widely spaced 10×10 meter squares. The seven assemblages were analyzed for numbers of different skeletal parts and vertebrate taxa. Theoretical and experimental evidence for the characteristics of bones as sedimentary particles formed the background for the analysis of the East Rudolf assemblages. The flume experiments of M. Voorhies (1969), plus measurements of whole-bone densities and settling velocities, supported the hypothesis that bones form distinctive dispersal groups when sorted by various taphonomic processes, especially fluvial transport. Therefore, the dispersal groups represented in fossil assemblages can indicate the taphonomic histories of these assemblages. Mammalian skeletal parts from the seven sample assemblages were analyzed for the percentages of different dispersal groups. The numbers of different parts were also

compared with the ratios of parts in a single, average skeleton. The fossil assemblages from fluvial deposits showed distinctive alteration from the ratios of parts in undisturbed skeletons. This resulted from the absence of the lighter bones which form the most easily transported dispersal group. The delta margin assemblages showed little alteration of bone percentages from those in an undisturbed skeleton, indicating little selective sorting prior to burial in this environment. The bones, hence the faunas, did not appear to be substantially mixed or transported from the general ecological province inhabited by the living animals. This information allows paleoecological inferences to be drawn from faunal distributions in the different environments. Faunal assemblages were analyzed for the patterns of occurrence of reptilian and mammalian groups. Aquatic and nonaquatic vertebrates (excluding fish) are preserved in approximately equal abundance in the delta margin deposits. Nonaquatic forms are significantly more abundant in the fluvial deposits. Several members of the mammalian faunas, particularly hippos, suids and bovids, show differential abundances in the two environments. Certain members of the Bovidae and Suidae have patterns of occurrence indicating preferences for delta margin or fluvial habitats. The paleoecologic information from the more abundant vertebrate groups helps to establish an ecological framework for the hominid fossils from the Koobi Fora Formation.

INTRODUCTION

The primary object of this study is to determine the paleoecology of vertebrate faunas that occur in the East Rudolf deposits of northern Kenya. Taphonomic analysis will provide the background for the paleoecologic interpretations. The crucial link between a fossil assemblage and the original ecosystem from which it was derived lies in the taphonomy of the assemblage, the history of its passage from the biosphere into the lithosphere. When bones of different animals are found together in a particular sedimentary deposit it is essential to know whether these bones were buried together because they were transported together (perhaps from different points of origin), or whether their close association indicates that the animals lived and died in the same habitat. The taphonomic history of a bone assemblage can provide this information.

Methods for establishing the taphonomic histories of fossil vertebrate assemblages in East Rudolf are explored and developed in this study in order to permit the fossil faunas to be related to former living vertebrate communities. These methods apply specifically to the East Rudolf bone assemblages, which represent thanatocoenoses (death assemblages) of large vertebrates that were disarticulated, fragmented and transported prior to burial. However, many of the conclusions concerning the interaction of these bones with processes of transport and weathering will have broad implications for paleoecologic interpretations of vertebrate assemblages from other regions and time periods.

This study consists of two major parts, the first providing theoretical and experimental models for the second, which analyzes particular bone assemblages from the East Rudolf deposits. The first part discusses factors contributing to bone dispersal and destruction in recent East African habitats and then examines in detail the properties of bones as sedimentary particles, including their dispersal potentials when subjected to fluid stress and their hydraulic equivalence to quartz particles. The second part describes the geologic context of East Rudolf bone assemblages sampled from seven different localities, analyzes their taphonomic histories, and then interprets the paleoecology of the faunas represented in each of the seven samples.

Many aspects of the East Rudolf region proved extremely advantageous as a background for the study of the taphonomy and paleoecology of a series of fossil vertebrate assemblages. The East Rudolf Research Expedition, led by R. E. Leakey of the National Museums of Kenya, has been active in the area since 1967 and has brought together a large team of scientists representing a wide range of disciplines. The collection of fossil vertebrates from the region as a whole has established the composition of the local Plio-Pleistocene faunas and has provided evidence for faunal

succession between about 4.5 and 1.3 my. B.P. The regional geology has been worked out through the combined efforts of several teams of geologists, and the overall stratigraphy and dating are reasonably well established. Archaeological investigations are providing evidence relating the cultural artifacts of primitive man to the broader context of the Plio-Pleistocene faunas and environments. In addition, the Recent faunas and environments of East Rudolf are comparable in many ways to those of the Plio-Pleistocene and serve as readily available analogues for the interpretation of the taphonomy and of the paleoecology of former time periods. A study of the recent taphonomy of lake margin areas is in progress (A. Hill, Bedford College, London) and this should give further valuable evidence for comparison with the fossil assemblages. On a broader scale, geological and palaeontologic information currently available for sedimentary deposits throughout East Africa, plus the wealth of data on the recent ecosystems, have greatly enhanced and broadened the scope of this study.

As an added attraction to all of the other advantages that characterize East Rudolf, the area is one of the richest known localities for fossil man. At present, over 120 specimens have been recovered, and these represent at least two taxa of contemporaneous, Plio-Pleistocene hominids. This study provides a background for the paleoecologic context of fossil man at East Rudolf in terms of faunal associations, environments, and possible habitat separation between the two forms.

The initial decision to undertake a study of the East Rudolf bone assemblages was in part inspired by previous, intriguing research in vertebrate paleoecology. The outstanding works that have helped to shape many of the viewpoints to be presented later include: Olson (1952, 1958), Shottwell (1955, 1963), Clark, Beerbower and Keitzke (1967), Voorhies (1969), and Dodson (1971, 1974). Information has been

drawn from various other studies relevant to the interpretation of assemblages consisting of bones of the larger vertebrates. These include the investigations of recent carcass decay and dispersal by Weigelt (1927) and Schäfer (1972). The overall theoretical background for taphonomy is derived primarily from Efremov (1940, 1953), the founding father of this line of scientific investigation.

Research on the East Rudolf bone assemblages and their relationships to different sedimentary environments was begun in the summer of 1971. Prior to this, I had spent two field seasons working on the stratigraphy and sedimentary environments of East Rudolf, as well as five weeks at Lothagam Hill on the southwest side of Lake Rudolf. Field work on the East Rudolf assemblages encompassed two field seasons of three months each in 1971 and 1972. Surface bones associated with different lithofacies were collected according to a consistent procedure that permitted later statistical comparisons between assemblages. All collecting and bone identifications were done by me or under my close supervision.

THE TAPHONOMY OF MACRO-VERTEBRATE ASSEMBLAGES

Many processes can influence the progression of bones from the living animal to the final place of burial and fossilization. All of these must be considered in order to derive paleoecological information from a fossil assemblage. Efremov (1940:85) applied the term *taphonomy* to this special area of geological and biological problems, and specified it as "the study of the transition (in all its details) of animal remains from the biosphere into the lithosphere." Processes included in taphonomy have been discussed in the general context of vertebrate assemblages by various authors (e.g., Efremov, 1940; 1953; Clark *et al.*, 1967; Müller, 1957). As an introduction to the study of the East Rudolf fossil assemblages, it will be useful to consider these processes

in some detail where they are relevant to the East African situation.

Factors Relating to Mode of Death

Causes of death initially determine which bones and which animals will have a potential for fossilization. Causes of death may include predation, disease, physical accident, poison, starvation and intraspecific strife (Clark *et al.*, 1967: 115). Predators have the greatest initial influence on the widespread dispersal of bones. Animals that die of other causes are likely to be similarly dispersed by scavengers, at least in East Africa, unless the carcass is somehow protected.

Lion, leopard, cheetah, hyaena, jackal, man and crocodile are the most important predator/scavenger members of the communities of large vertebrates in East Africa today. All of these both hunt and scavenge (Kruuk, 1972; Van Lawick-Goodall, 1971; Schaller, 1972). Vultures also are important contributors to bone dispersal. The effects of these predators and scavengers on a carcass are referred to as "carnivore activity" in the following discussion. Disassociation of a skeleton can be amazingly rapid and thorough. Kruuk (1972:126) reports that a young wildebeest killed by hyaenas had its parts completely dispersed from the site in 13 minutes. Both hyaenas and lions will kill in shallow water and may have their meal there rather than dragging the carcass onto land. However, lions often will drag whole carcasses or parts away from the site of death. Hyaenas may carry favorite parts long distances (away from other hyaenas). Kruuk (1972:119) observed hyaenas caching parts of carcasses in 30–50 cm of standing water, with variable success in retrieving the cache later on. When a shallow pool dried up, many bones were exposed, apparently as a result of this behavior.

The preferences of carnivores for consuming particular parts of a carcass have an important bearing on what would remain to be fossilized and which bones would be

PROCESSES IN VERTEBRATE TAPHONOMY

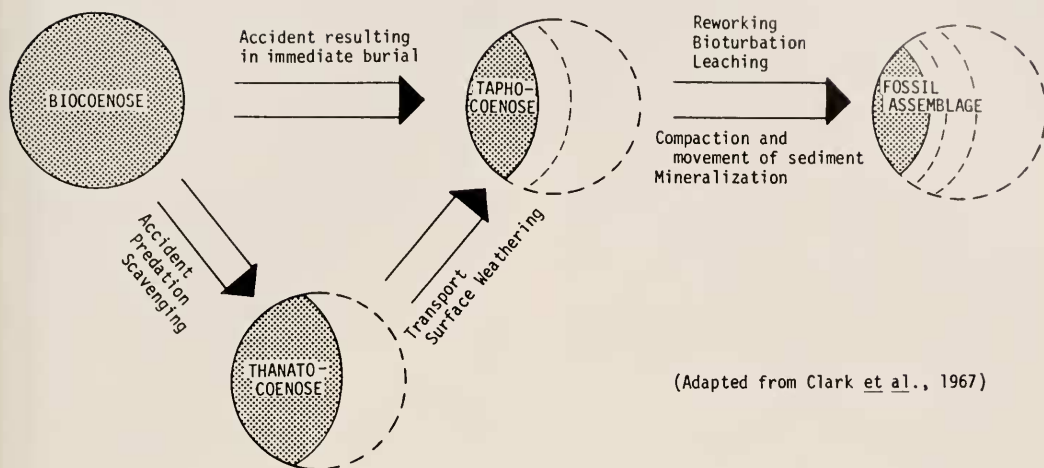


Figure 1.

likely to remain near the site of death. Kruuk (1972:126) reports: "If any part of a corpse is left by hyaenas in both Ngorongoro and Serengeti, the skull is most likely to remain uneaten, followed by the vertebrae, ribs, pelvis and ends of long leg bones." Lions will also consume everything but "horns, teeth and a few bone splinters and scraps," of small prey such as gazelle (Schaller, 1972:269). Carnivore activity by man would probably result in less total destruction of bones, but limb shafts might be split for marrow and skulls broken open for the brain (White, 1955, Brain, 1967b).

It is obvious that a crucial factor in the number of bones which survive to become a thanatocoenose (death assemblage) will be the proportion of carnivores to the number of food animals at any one time. In Kruuk's study areas, the number of predators was high, and the number of carcasses left intact was low. Observations of carcasses in the East Rudolf region reveal a fairly large number of intact or partial skeletons, reflecting a relatively low number of carnivores. The reciprocal relationship between numbers of carnivores and numbers of complete bones or carcasses has been

generally noted in East Africa (e.g., Estes, 1967:39).

Not only numbers, but relative sizes of carnivores as well as their degree of adaptation for bone mastication will have important effects on a thanatocoenose. The strength of bones with nutritional value must exceed the crushing force of the jaws of hyaenas and lions in order to remain intact, unless there is a surplus of food (e.g., mass deaths), which would make bones less attractive food items.

Crocodile predation or scavenging will tend to bring bones into close association with depositional environments but may totally destroy bones that are consumed. The proportion of large animals in a crocodile's diet increases with its size, and prey can range up to the size of an adult black rhino (Selous, 1908:201). Crocodiles generally kill by dragging animals into the water and drowning them. They are also active scavengers, ranging as much as half a mile from water, and may even compete with lions for a kill (Cott, 1961:302-303). Carcasses are torn apart or may be cached (underwater) until decomposition makes dismembering easier (Guggisberg, 1972:

94). Bones and teeth are demineralized during digestion, and remaining organic material (mainly collagen) disintegrates rapidly after defecation (D. Fisher, personal communication). Thus, only bones that are too large or cumbersome to ingest (e.g., skulls), or that are neglected by the crocodile, would survive. However, these would have optimal chances for burial.

Drowning, disease, starvation and other causes leading to mass deaths can have different effects on a thanatocoenose. Any mass death situation is likely to create a surfeit of food for the local carnivores, and many skeletons may be left more or less intact. Schaller (1972:215) notes that lions do not seem to scavenge from such deaths. It takes only a short time for carcasses to mummify in dry conditions and become unattractive to most scavengers. Once mummified, a carcass could probably survive a certain degree of transport without becoming disarticulated.

Mass death by drowning seems to be fairly common among the East African ungulate species. The social behavior of herd-oriented species (e.g., zebra, wildebeest) can result in mass panics in which the fright of a single animal may cause a group stampede. Such events often occur at waterholes, and many animals may be trampled and drowned (R. Estes, personal communication). Schaller (1972:215) reports the death of 62 wildebeest in a waterhole at one time, and 83 in the same place a few years later. Apparently many herd-oriented animals also drown during river crossings. Abel (1912:12) mentions panic as one of the causes of massed vertebrate remains, but the idea has not generally been used in the interpretation of massed fossil assemblages.

In a discussion of the causes of mass deaths leading to fossilization, Kurtén (1953:72) favors seasonally occurring floods or, in a more general sense, linked causes of death and deposition. Voorhies (1969:52) supports a catastrophic event of this kind in the case of the Pliocene Verdigris

Quarry in Nebraska, and suggests large-scale drought or winter storm followed by flash-flooding as the cause of the deposit. Drought may concentrate animals that are not normally herd oriented. However, in some cases it would be worth considering social catastrophes as well as climatic events in interpreting massed assemblages of fossil vertebrates.

The drowning of single animals, as in river crossings, initially provides good conditions for the burial of a whole skeleton or articulated parts. Scavenging by crocodiles, and possibly also by fish and turtles, can destroy such carcasses, and if they float long enough to decay, various parts may gradually drop off and be widely dispersed. However, drowning can lead to the preservation of whole or partial skeletons. As a consequence, wildebeest, and other non-aquatic animals, might be among the best preserved fossils in channel and point-bar deposits.

The above observations are relevant to paleoecological interpretations based on the preservation of vertebrates in channel and point-bar deposits. Dodson (1971:69) has suggested that the excellent, complete preservation of hadrosaur skeletons in the channel deposits of the Oldman Formation (western Canada, Cretaceous) indicates that a good portion of the hadrosaurs' time was spent living in the channels. By analogy, it might be possible to conclude that wildebeest occupy aquatic habitats, based on where the most complete skeletons would be preserved. The fact is that wildebeest are terrestrial in their habits, but occasionally die in channels. In many cases, the exception (e.g., drowning) may produce the fossil, while "normal" habits will leave little or no record. The hadrosaurs may have been partly aquatic, but their place and state of preservation in the channel deposits should be used only in support of other evidence for aquatic habits.

In general, it appears that two major kinds of thanatocoenoses can be derived from modern large-vertebrate communities;

an incomplete, broken and dispersed one resulting from carnivore activity, and a relatively complete one (in terms of whole bones and associated skeletons) resulting from mass deaths. The first can form fossil assemblages which sample faunas over periods of months or years, while the second may lead to assemblages which sample the standing crop of vertebrates at specific points in time. Intermediate kinds of thanatocoenoses will depend on the numbers of carnivores and the effects of scavenging on the available carcasses.

In East Africa today, many thanatocoenoses are composed of broken and incomplete skeletons, owing to the large numbers of carnivores. The parts that are left to continue toward fossilization chiefly include skulls, horn cores, vertebrae, ribs, ends of limb bones and teeth, *of the larger animals* (primarily ungulates). These are subjected to weathering and transport and are treated as sedimentary particles by the various geologic processes. More complete carcasses occur in situations where they are not subject to scavenging. From the recent evidence, it appears that a thanatocoenose composed of fragmented skeletons is likely to occur in an area broadly representative of the habitats of the living animals, although later the bones may be dispersed from the area by fluvial processes. A thanatocoenose composed of massed, complete skeletons is more likely to represent localized conditions of death and/or transport. Thus, a fossil assemblage composed of bones from a fragmented thanatocoenose *that has not been transported* should preserve the best evidence for the paleoecology of the fauna.

The foregoing discussion applies to the larger vertebrates, and it is assumed that the bones of animals of sheep size and smaller will be much less likely to survive carnivore activity. However, small vertebrates such as turtles and fish probably form thanatocoenoses comparable to those of the large mammals and reptiles, reflecting both carnivore activity and occasional

mass deaths. Processes leading to thanatocoenoses composed of small mammals are not well understood and are worthy of further investigation. However, since the East Rudolf deposits have so far yielded a negligible number of small mammals, such an investigation will not be undertaken in this study.

Factors Relating to Weathering and Decomposition

The biological and chemical properties of the place where an animal dies will have an important effect on bone destruction. Humid surface environments will facilitate the decay of organic material and will cause dissolution of bone minerals. Dry environments dehydrate the organic component of fresh bones, resulting in cracking and splitting. For the most part, since teeth have less residual organic matter, they will survive surface weathering better than other parts, although large teeth tend to split when dehydrated.

The rate of decay of muscles and ligaments is of interest in determining how long parts will remain articulated. In the absence of vertebrate carnivores, insect activity is an important process in defleshing a skeleton and is enhanced by warm, humid, subaerial conditions. In such conditions (summer in South Carolina, U.S.A.), Payne (1965:597) has observed complete removal of flesh from the carcass of a baby pig in eight days when insects were present, but flesh remained after 100 days when insects were absent. Voorhies observed sheep carcasses in the drier conditions of Nebraska and reports complete disarticulation after 90 days of normal insect activity. Carcasses of mammals that are submerged in water may disarticulate in 1 to 3 months (Dodson, 1974:79; Schäfer, 1972:21). The evidence suggests that the most rapid rates of disarticulation owing to insects and the activity of micro-organisms may be achieved on land. However, under certain conditions, bones can remain articu-

lated for weeks or months in either sub-aerial or aquatic environments.

Very little is known about the textural characteristics of bones weathered under different conditions. However, there is some data on the length of time bones can survive surface weathering. Voorhies (1969: 31) reports that bones left for a year in the Nebraska climate were soft and cracked, showing noticeable signs of disintegration. Bone-weathering experiments in East Africa show nearly complete destruction in 7 to 8 years (Isaac, 1967:40). Observations on bones in various East African game parks indicate they can last several years, but are usually in good condition for only a few months (A. Hill, personal communication). In the semi-arid climate of Lake Rudolf (annual rainfall ~ 250 mm [10 inches]), bones acquire distinctive characters indicative of surface weathering, including flaking, splitting and splintering (Plate 1) during the first few months of exposure. Bone is evidently a very short-lived material in surface environments, and must be left in actively aggrading depositional situations in order to survive intact. If bones are to maintain a fresh and unweathered appearance, they must be buried soon after the death of an animal.

The characteristic appearance of naturally weathered bone surfaces is often distinguishable after they have been fossilized. This can provide invaluable evidence for the taphonomic history of a bone or bone assemblage. Typical surface textures are shown in Plate 1. Certain types of fractures also appear to result only from breakage in fresh bones. These include spiral, fibrous and sawtooth fractures as shown in Plate 2. Some work has been done on the characteristic weathering and fracture patterns of bones (e.g., Sadek-Kooros, 1966; Brain, 1967a; Reif, 1971). Preliminary experiments using tumbling mills show that bones can be abraded and rounded during transport without extensive fragmentation. Projections on the bones are usually broken off and surfaces become smooth and rounded

(G. Jepsen, personal communication). More experimental work is needed in order to establish the causes of the observed fracture patterns and surface textures of recent bones.

The major factor determining bone appearance and survival potential under surface conditions appears to be the content of organic matter. Crystals of hydroxyapatite which form bone are supported in an extensive system of organic material. Bones that have this organic material removed artificially can be reduced to powder with very little force (a vertebra can be crushed in one's hand). Bones that have been demineralized, leaving only the organic material (principally collagen), maintain their form and can be bent and twisted like rubber (F. A. Jenkins, Jr., personal communication). Weathered bones that have obviously lost much of their organic content can be easily crushed and broken and are particularly friable when wet, with relative strength proportional to the compactness of the bone structure. These bones would be easily abraded and destroyed in transport situations, while bones with greater residual organic content would survive longer under similar conditions.

Bone can be regarded as a very labile kind of sedimentary particle that is characteristically altered by the geologic processes to which it is subjected. Therefore, bones may reveal a great deal about the influence of weathering and transport on their pre-burial history.

Transport and Burial

Bones can be transported from the place of death either within a floating carcass or as isolated objects that behave as discrete sedimentary particles. Flotation could lead to considerable transport of bones away from the habitat of the living animal with little damage to bone surfaces. There are no experimental data as yet to show how far isolated bones can be transported. However, a certain amount of information can be derived from a theoretical consideration

of the properties of bones as sedimentary particles. These will be given detailed examination in the following chapter, since an understanding of bone transport is crucial for paleoecological interpretations from assemblages of isolated bones such as those found in the deposits of East Rudolf.

Whole or nearly whole carcasses can be floated intact to places of deposition as long as gases remain trapped inside (Schäfer, 1972). In East Africa today, transport of floating carcasses for long distances is probably rare owing to the prevalence of crocodiles. However, in at least one case, long-distance carcass transport has been observed. A skeleton of a topi (*Damaliscus*) was found on the shores of North Island in the center of Lake Rudolf, 24 km. (15 miles) from land across waters in which crocodiles are abundant (I. Findlater, personal communication).

Transport of articulated parts that do not float will also occur. Ligament softens when immersed in water but may still hold bones together, particularly body parts such as feet and limb joints (Dodson, 1974:79). The principal factors limiting long-distance transport of articulated parts would be the rate of ligament decay and the combined size and shape of the object.

The place where an animal dies will have a great effect on the dispersal potential of its bones. For example, a skeleton lying in dense bush on a floodplain or levee has a lower chance for dispersal than one on open flats, simply because of the obstruction caused by vegetation. The trapping effect of vegetation, particularly along levees, would greatly reduce the probability of transporting bones from floodplains to channels or vice-versa. Levees might effectively trap bones during flood stages when the potential for burial is high, and thus would preserve a mixed or allochthonous fauna. Bones of animals that actually died on the levees would be preserved there only if they were buried before being destroyed by surface weathering. On the deltas, recent examples show a trapping

and binding effect of grasses on bones which would prevent their movement unless the vegetation was destroyed (Plate 3).

Transport of parts of carcasses and isolated bones by predators and scavengers is also a factor in bone dispersal. This may be significant for individual carcasses, but it is probably not effective in moving an entire thanatocoenose away from the general area of the biocoenose, at least for large animals with fairly broad habitats. Specific cases may be important taphonomically, such as the dispersal of fish and crocodile remains away from aquatic environments by carnivore activity.

Re-excavation of buried bone is potentially important in floodplain situations with laterally eroding and aggrading channels and in lacustrine transgressions involving erosion of former shoreline deposits. Experimental evidence¹ shows that bones continue to lose organic matter (presumably used by soil bacteria) after burial and become very soft and friable after a few years of burial in wet sediment. Re-excavation would rapidly destroy all but the most durable parts, leaving teeth and compact bone fragments. Beaches or channels that erode into previous deposits would tend to concentrate teeth and the most durable bone fragments and redeposit them. In some cases, bones might become well enough mineralized during burial to survive re-excavation intact, particularly if they were protected by carbonate concentrations formed in floodplain or levee soils.

¹Experiments are in progress on the shore of Lake Rudolf, where controlled samples of recent bone have been buried below the water table. These were examined in 1970 and 1972 for changes in color, weight, and surface texture. All ligaments joining originally articulated parts disappeared after one year of burial. After two years of burial, bones had lost 10–20% of their dry weight (loss of organic material) and had acquired a characteristic brown patina on their external surfaces. Otherwise there was minimal change in appearance, but all bones were soft and friable.

Diagenetic Factors

Bones can be destroyed after burial by a variety of processes. Bioturbation, in which sediment is mixed by the action of roots and burrowers, is probably an important factor in some cases of bone destruction. Once bone is softened underground by the loss of organic matter and by ground water, it could easily be penetrated and disrupted by the agents of bioturbation. This may account for the observed low frequency of bones in paleosol horizons in the East Rudolf deposits. In floodplain deposits, bones would be best preserved when the increments of sediment added during a flood were thicker than the average depth (e.g., 10–50 cm) of the root and burrow penetration that would affect the new land surface. Accumulations of this magnitude have been observed after a single major flood of a small river in central Colorado (McKee *et al.*, 1967:835). Rapidly aggrading floodplains lacking extensive plant cover would provide an ideal depositional situation for preserving floodplain thanatocoenoses with minimal subsurface destruction.

Compaction of sediment can crush and distort buried bones, particularly if they are wet and friable because of subsurface conditions. Distortion could occur if the bones are somehow decalcified and rubbery or if organic material has been lost, leaving a fragile structure of hydroxyapatite crystallites. The effects of compaction will be greater in clay-rich sediments that lose a significant volume of water when compacted. Clay units also may undergo a considerable degree of expansion and contraction, creating minor slickensides and joint systems. As noted by Dodson (1971:55) this can cause breakage of enclosed bones, although the broken pieces may themselves be well preserved (B. Patterson, personal communication). Sandy units are less subject to compaction and fracturing, and enclosed bones will be less disturbed. Thus, for purely physical reasons relating to sediment type, bones buried in clays and

silty clays will have much less chance of undisturbed preservation than bones buried in coarser sediments.

An abundance of CaCO_3 in a deposit, or the seasonal movements of ground water charged with a Ca^{++} and CO_2 , may either help to preserve a buried bone or to destroy it. Bones can serve as centers of CaCO_3 nodule formation and are often permineralized with CaCO_3 . In some cases, however, bones can be “exploded” by the outward growth of a carbonate nodule. East Rudolf fossils provide examples of this as well as bones which have breaks that are “healed” by CaCO_3 deposits. The processes of carbonate deposition in association with bones are poorly known. In some cases the original apatite is not altered by fossilization, as shown by unaltered carbon contents of recently fossilized bone apatite (Haynes, 1968). There is some evidence that the amount of organic matter in a buried bone will influence its fossilization, with fresher bones tending to encourage nodule formation (Konizeski, 1957:141). Environments with locally high concentrations of calcium, such as those associated with high-calcium vulcanism in the East African Rift System (Bishop, 1968:38), seem to promote thorough permineralization of bones and later resistance to surface destruction of the fossils.

Carbonate concentrations imply fairly alkaline soil conditions (Millar *et al.*, 1966:143), which will be more likely to preserve bone than acid conditions. Rates for the dissolution of bones in association with acid soils are not known, but over time, even slight acidity (undersaturation of Ca^{++}) would contribute to their destruction.

Conclusions

The points of taphonomic interest for the interpretation of East Rudolf (and other) fossil assemblages include the following:

- 1) Mode of death will be of primary importance in determining which skeletal parts will be available for

fossilization. When carnivores exert their maximum effect on carcasses of relatively large animals (> 150 kg), skulls will be the most common residue, followed by vertebrae, ribs, pelvises, and ends of long bones. Smaller animals may be destroyed entirely except for teeth and parts such as horn cores. Burial of articulated skeletons will occur rarely, and then only when scavenging is held to a minimum. The proportion of complete bones that survive scavenging will be a function of the density of carnivores in relation to prey at any particular place and time; the greater the carnivore density, the fewer the complete bones.

- 2) Terrestrial animals may have the best chances for complete preservation in environments that are not their normal habitat (e.g., drowned wildebeest buried in channel deposits). The parts of a thanatocoenose that are *not* subject to immediate transport will be the most useful in reconstructing a biocoenose. Once bones are disarticulated and exposed to weathering, their chances for dispersal away from the immediate area, without significant alteration of the thanatocoenose, are greatly reduced. Dispersal potentials are then dependent on the size, density and weight of each bone and its rate of destruction *in situ* or in transport.
- 3) Bones quickly show the effects of surface weathering after initial exposure (usually a matter of weeks or months), and they will not last more than 3 to 10 years under most surface conditions in any sort of intact state. Fossil bones with intact fresh-appearing surfaces were probably buried relatively soon after the death of the animal.
- 4) Teeth should outlast bones in most taphonomic situations, and small teeth will probably have a higher survival potential than large. Compact bone

weathers and abrades more slowly than porous. Bones that have lost a good proportion of their residual organic content (collagen) will be more quickly abraded and destroyed during transport than fresh bones.

- 5) Well-preserved fossil bones record the fact that the deposit they are in has not been extensively reworked. Reworking should result in the fragmentation or total destruction of bones unless they are thoroughly mineralized. However, teeth may survive and be concentrated from older deposits.
- 6) Buried bones can be disrupted or destroyed by bioturbation, acid ground water, carbonate nodule formation, and movement of enclosing sediment with a high clay content. Alkaline conditions with available CaCO_3 are an optimal chemical environment for bone preservation.

CHARACTERISTICS OF RECENT BONES AS SEDIMENTARY PARTICLES

Vertebrate remains can be transported along with other material moving from place to place on the earth's surface. Bones from different sources can be mixed, and some can be carried long distances while others lag behind. In order to determine the ecological provenance of the bones, it is first necessary to understand their behavior in transport situations.

A few experiments have been done on bone transport under controlled conditions in laboratory flumes. Voorhies' (1969) study on the transport of disarticulated sheep and coyote skeletons provides data on bones of moderately large vertebrates. Dodson (1974) conducted flume experiments on the dispersal of mouse bones. His data show that mouse bones can be easily transported by relatively low velocity currents (6–35 cm/sec.), and he concludes that dispersal will be so great as to render the bones essentially useless for paleoecologic

TABLE 1. VOORHIES DISPERSAL GROUPS: BONES OF SHEEP AND COYOTE WHICH ARE TRANSPORTED TOGETHER IN A FLUME WITH CURRENT VELOCITIES UP TO 152 CM/SEC.

<u>GROUP I</u>	<u>GROUP II</u>	<u>GROUP III</u>
Immediately transported by flotation or by saltation.	Transported later than Group I, usually by traction.	Resisted transport, lagging far behind other groups.
RIBS	FEMUR	SKULL
VERTEBRA	TIBIA	MANDIBLE
SACRUM	HUMERUS	(ramus)
STERNUM	METAPODIAL	
(scapula)	PELVIS	
(phalanx)	RADIUS	
(ulna)	(scapula)	
	(ramus)	
	(phalanx)	
	(ulna)	

Parentheses indicate occurrence in more than one group.

(From Voorhies, 1969)

interpretations (Dodson, 1973:82). However, Voorhies' data show that most sheep and coyote bones require greater current velocities to move, and that distinct groups of bones with different dispersal potentials form at velocities comparable to those found in natural streams (~ 20–150 cm/sec. (Leopold *et al.*, 1964:166)).

The dispersal groups of bones (referred to as "Voorhies Groups"), are shown in Table 1. These are formed of skeletal parts that tend to be transported together as the current velocity in a flume is increased to a maximum of 152 cm/sec. Fifteen separate trials were run and the results averaged to give the three dispersal groups (Voorhies, 1969:66).

Voorhies' work shows that different bones require different minimum fluid shear stresses for transport. This provides a valuable basis for interpreting fossil assemblages

of bones of sheep and coyote size. An assemblage composed primarily of either Group I, Group II or Group III would indicate that sorting processes related to transport had been operating on the original thanatocoenose. An assemblage composed of Group III would retain more paleoecologic information than one consisting of Group I or II, since this group requires the greatest stress for transport.

The flume data are restricted to sheep and coyote bones and provide little direct information on how bones of other animals, of other sizes, will sort under current action. However, Voorhies' data can be used to indicate the relative importance of basic characters of bones in forming the dispersal groups. These characters are size, density and shape, the important parameters of any sedimentary particle. In order to show how these parameters affect bone transport, it

is necessary to understand how they affect the transport of sedimentary particles in general. The principles and formulae that describe fluid-particle interactions are reviewed in a number of recent texts, and references used for this study include J. Allen (1970), Pettijohn *et al.* (1972), and Shapiro (1961).

Properties of Bones as Sedimentary Particles

Data on the sizes, densities and shapes of bones are necessary for a theoretical consideration of bones as sedimentary particles. Since there is little or no information of this kind available, it was necessary to carry out a series of measurements to determine the general range of densities and sizes (volumes and weights) of bones. These provide the basis for subsequent discussion of bone transport potentials.

MEASUREMENTS OF BONE SIZE AND DENSITY

In order to relate the characters of measured bones to the East Rudolf fossil assemblages, bones of recent representatives of fossil taxa were used. These included museum skeletons of hippopotamus, zebra, a large and a small antelope (*Redunca*, *Damaliscus*), and a pig (*Hylchoerus*), as well as parts of two crocodiles and various fish species. In addition, the skeleton of a sheep was used for comparison of size and density characters with Voorhies' flume data. The bones included variable amounts of residual organic material, but in general were thoroughly degreased.

Volumes and weights were measured for each bone. Volumes were measured by a simple water-displacement method. Bones were soaked for 5 minutes, or until bubbling stopped, and then measured for volume which included the absorbed water. Wet-weight, also including this water, was measured, in order to derive a wet density for each bone. Wet density is the parameter of interest if bones are transported while wet and take up water quickly upon

immersion. Rates of water uptake will be discussed further below.

Densities, weights and volumes of most of the skeletal parts of the animals listed above are given in Appendix 1. In general, densities range from less than 1.0 to about 2.3, volumes from 1.0 to 3000 cc, and weights from 1.5 to 4900 grams (g). Bone densities are comparable for all mammals except hippos, which are generally slightly higher. Crocodile and fish bones have generally higher densities than mammal bones. Within each skeleton, the range of densities is very broad, from foot bones and vertebrae that float to teeth, which are the heaviest parts for their size.

How representative are these measurements of bones that are actually parts of natural thanatocoenoses? Several possible sources of error can be examined and their overall importance analyzed:

- 1) *Differential uptake of water.* It was apparent during the measurements of volumes that bones varied in their rates of immediate water absorption. Some floated for several hours with essentially no water gain, while others were immediately permeated. In nearly all cases the major weight gain from water uptake occurred in the first 1-5 minutes of immersion. Figure 2 shows the rates of water absorption for various bones. It is significant that the naturally weathered bovid femur gained all of its water in the first moments of immersion, while the museum femur continued to gain weight after 70 hours of soaking. This indicates air pockets in the unweathered bones which are probably blocked by organic matter. All pores are open in the weathered bone and water quickly permeates it.

Naturally occurring, unweathered bones also will have trapped air pockets that can lower their densities during initial transport. However, the rates of surface weathering are rapid enough so that most exposed bone

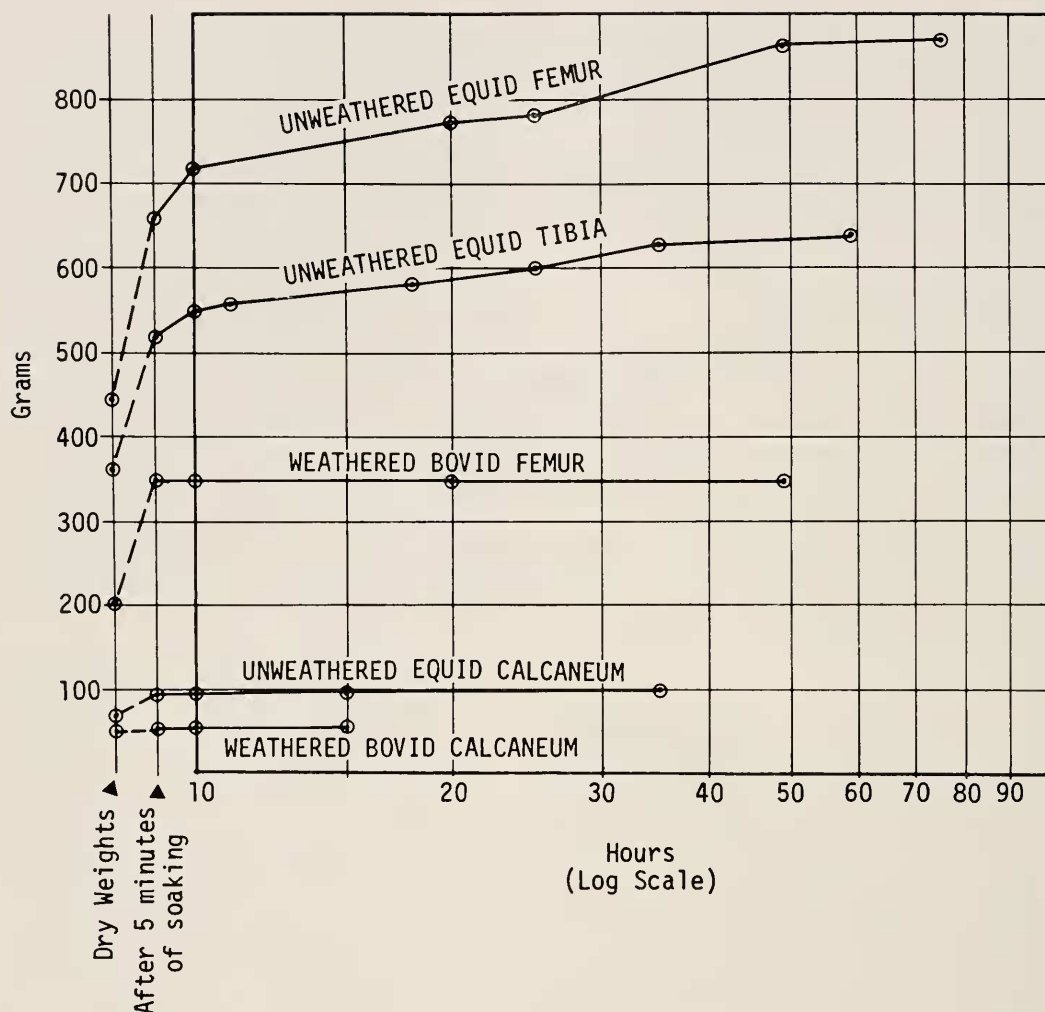


Figure 2. Water uptake rates of different mammal bones. Weathered bones and small or compact bones gain essentially all of their water content within five minutes of soaking. Large, unweathered bones with residual organic matter gain weight more slowly as pockets of trapped air are gradually displaced.

would become permeable in a matter of a few months. Therefore, the museum assemblage differs from natural ones in its greater number of blocked pore spaces, which will tend to lower the measured densities. For the larger and more porous parts, the wet weights and densities recorded in Appendix 1 are thus *minimum* estimates of these measures for naturally weathered bones.

2) *The original organic content of the*

bones. Aside from contributing to air entrapment in a bone, residual organic matter probably does little to affect its overall weight and density. The density of cartilage is 1.1 and tendon 1.3 (Currey, 1970:30). Other tissues have densities close to 1.0 since they are composed primarily of water. A bone filled with water should have about the same weight as a bone filled with tissue, and after initial submergence, the two would have

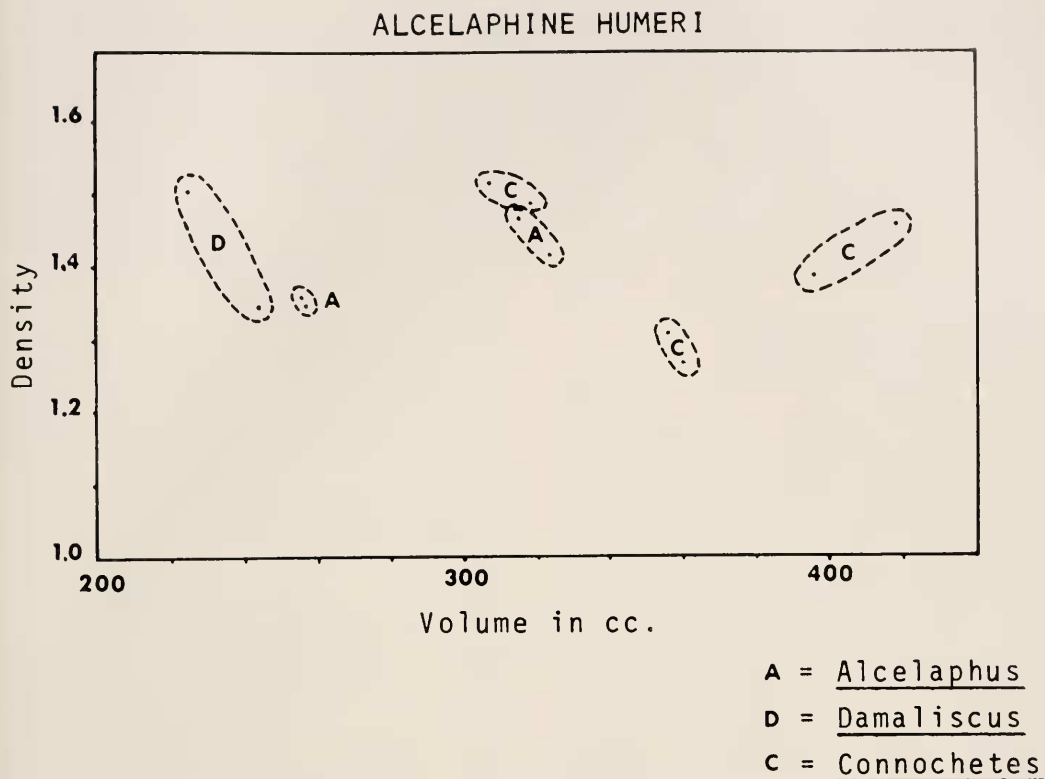


Figure 3. Graphs showing density variation in a sample of 12 alcelaphine humeri. Dotted lines encircle the left and right bones from the same animal. Density differences between right and left of a pair are due to variation in the amount of air initially trapped in the bones. Density differences between pairs may be due in part to original variations in the amount of bone per cubic centimeter in the individual animals.

approximately the same density, other factors being equal.

- 3) *Variations in bones from different individuals.* The same skeletal part may vary in density in individuals of the same group of animals because of body size, age, diet, etc. How great is this variation? A series of humeri from a single bovid group were measured in order to answer this question. Figure 3 shows that the humeri vary from 1.27 to 1.52 in density. Density variations owing to differential water uptake are indicated by the differences between right and left sides. Compared with the range in volume, there is relatively little variation in the densities of humeri from the different genera. It

appears that differential uptake of water is more important in affecting the densities of fresh bones than variations between individuals of different sizes or genera. Experimental work on the density variations of weathered bones should be done, but it seems probable that individual variation in similar skeletal parts is not an important factor affecting bone dispersal potentials.

- 4) *Experimental error.* Repeated trials showed this to be much less than other causes of density and weight variation. The error was generally less than 5 percent for wet weight and volume.

The differential uptake of water in fresh

bones appears to be the major factor that may cause the measurements given in Appendix 1 to be different (i.e., lower) than the actual properties of naturally occurring, waterlogged bones. Measurements of weights and densities of weathered bones and thoroughly waterlogged fresh bones (Fig. 2) indicate that the densities given in Appendix 1 are within about 15 percent of the true densities for large, porous bones and are much closer for smaller, more compact ones.

Published data on bone density indicates a range similar to that given in Appendix 1. Samples of porous (cancellous) and compact (cortex) human bone have densities of 1.78 and 1.88, respectively (Johnson, 1965:550). Currey (1970:30) lists the specific gravity of "bone" as 2.0, "ear bone" (= petrous part of temporal) as 2.4 and tooth enamel as 2.6. The density of the bone mineral, hydroxyapatite, is 3.1 to 3.2 (Berry and Mason, 1959:454). (Published determinations of bone density usually relate to a cubic centimeter of average boney material, not the bulk density of whole bones, which is less owing to the number of naturally occurring open spaces and the presence of trapped air pockets.)

From the above discussion, it can be concluded that measurements of bone size and density as given in Appendix 1 are generally representative of the variation that would be present in a natural bone assemblage, and they can be used to predict hydraulic behavior if the limitations of the data are kept in mind. For the following discussion of the relative dispersal potentials of bones, absolute measures of bone density, etc., are less important than consistent differences in the *relative* properties of different skeletal parts.

Relative Dispersal Potential of Bones

How does the dispersal potential (probability of transport) of bones relate to characters of size, density and shape? This can be shown by plotting density versus wet weight for all the skeletal parts of the

sheep, as given in Appendix 1, and comparing the distribution of bones with the Voorhies Groups. Figure 4 shows that Group I consists of the smallest, lowest density bones. Groups II and III are composed of bones that are denser than those of Group I but not necessarily larger. Density appears to be more important than size in determining whether bones will disperse with Group I.

The scapula and mandibular ramus (with teeth) fall within Group II on Figure 4 although they do not always belong there according to the flume experiments (Table 1). The scapula can belong to Group 1, yet its size and density do not show this. The shape factor must be operating to increase the dispersal potential of the scapula, and this is reasonable considering its high surface area to volume ratio. Its form, with the spine projecting at right angles to the scapular blade, also would contribute to bottom instability. The ramus, on the other hand, is more of a lag element (Group III) than its size and density indicate. Its surface area to volume ratio is fairly high, and this should operate to make it more transportable. However, as noted by Voorhies (1969:67), rami have a convex-up (buccal side up) stable bottom position and are relatively flat. Once they attain a stable bottom position, the size and density combine with a relatively small cross-sectional area (as seen by the current) to decrease transport potential.

It is clear that density and size characters of bones can explain their dispersal potential as shown by Voorhies Groups, with shape becoming an important factor only for particular bones. Although natural transport conditions will vary greatly from those of the flume, the sorting of groups of bones with different transport potentials would seem an inevitable consequence of their differences in size, density and shape. Dispersal groups of bones of sheep size and above should form at current velocities found in natural flow conditions, unless these flows are competent enough to carry

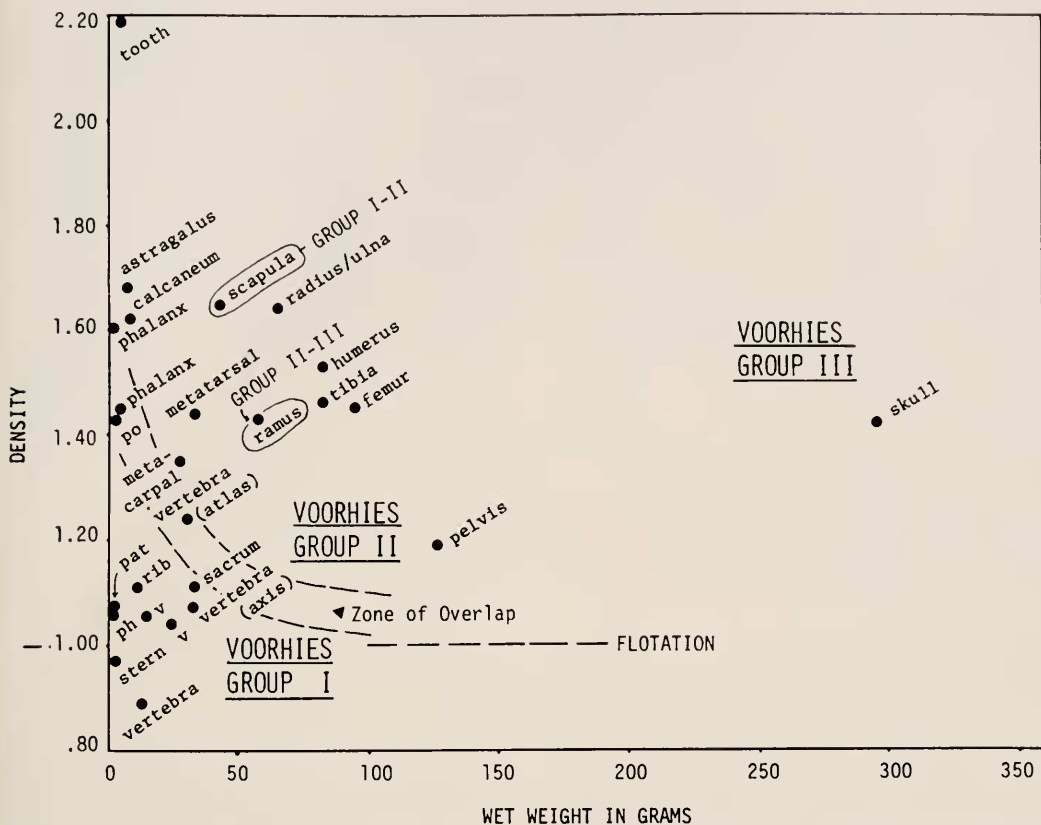


Figure 4. Plot of density versus wet weight for sheep bones showing that these two variables can be related to the Voorhies Dispersal Groups. Group I is the most easily transported according to Voorhies' flume experiments, and Group I elements have low densities and/or weights. The scapula and ramus, which do not plot within their dispersal group, indicate that shape has an important effect in their potential for transport under fluid stress. Abbreviations: po = podial, pat = patella, v = vertebra, ph = phalanx, stern = sternum.

all bones together (e.g., high density mud-flows).

Using density and weight data for the other animals given in Appendix 1, it is possible to predict, in general, which bones of these animals would sort out with Voorhies Groups I, II and III, under the same experimental conditions. Those elements which fall in the Group I zone and in the mixed Groups I/II zone are listed for each animal in Table 2. If these were placed in the flume with the sheep bones, their size and density should cause them to sort out with the easily dispersed group, and they would be transported away from the other skeletal parts. For the different

animals, the same skeletal parts are consistently present in Group I, but the number of Group I elements decreases with increased animal size.

Since Voorhies Group I is the most easily affected by transport, its presence or absence in fossil assemblages can provide specific information on the sedimentary history of these assemblages. For example, if one of the East Rudolf assemblages were composed only of bovid vertebrae and ribs, equid vertebrae, terminal phalanges of hippos, etc., then this would almost surely represent a transported, allochthonous bone concentration. Various models of this kind can be constructed for later comparison

TABLE 2. BONES OF DIFFERENT SIZED RECENT ANIMALS WHICH SHOULD DISPERSE AS VOORHIES GROUP I OR GROUP I II UNDER FLUID STRESS. THE DISPERSAL POTENTIAL OF MOST OF THESE BONES IS DETERMINED BY THEIR LOW WEIGHT AND/OR DENSITY. ALL OTHER BONES SHOULD LAG BEHIND. BONES IN GROUP I/II ARE SHOWN IN LOWER CASE.

OVIS	REDUNCINE	SUID	ALCELAPHINE	EQUUS	HIPPO	CROCODYLUS	FISH
Phalanges	Ulna	Podial	Phalanges(t)	Calcaneum	Phalanges(t)	Scutes	Pectoral
Sacrum	Podial	Phalanges	Rib	Podials	Sesamoids	--	Spine
Sternum	Sacrum	Patella	Ulna-P	Phalanges	--	scutes	(Bagrus)
Vertebrae	Vertebrae	Sesamoids	Vert. Cent.	Vertebrae	phalanges(t)	small	Skull
Axis	Atlas	--	Sesamoids	Cervical	phalanges	teeth	(Lates)
Cervical	Axis	rib	--	Lumbar	sesamoids		--
Thoracic	Cervical	astragalus	podial	Patella			pectoral
Lumbar	Thoracic	podial	phalanges	Vert. Cent.			pectoral
Patella	Patella	phalanges	vertebrae	Sesamoids			+ spine
Humerus-P	Ulna-P		cervical	--			skull parts
Metacarp-D	Vert. Cent.		lumbar	vert.-thor.			(Clarius)
Vert. Cent.	Sesamoids		patella	rib			
Rib	Phalanges		rib	calcaneum			
Sesamoids	--			astragalus			
--	calcaneum						
astragalus	phalanges						
podial	vert.-lumb.						
vert.-atlas	rib						
metatars-P							
metacarp-P							
phalanges							

Vert. = Vertebra
(t) = Terminal
P = Proximal
D = Distal

with the fossil assemblages. These are summarized in Figure 5. Three basic kinds of assemblages can occur, with transitional phases: "undisturbed" (Groups I, II, III), "winnowed" and "lag" (Groups II, III), or "transported" (Group I), in decreasing order of paleoecological importance.

The proportions of different Voorhies Groups in fossil assemblages should provide evidence for the proximity of fossils to the original thanatocoenose and the habitats of the living animals. This is a different approach from that of Shotwell (1955, 1963), who attempted to distinguish proximal and distal (more transported) paleocommunities on the basis of numbers of different skeletal parts representing each fossil taxon. The basis for Shotwell's method was the idea that the proximity of an animal's habitat to the site of deposition would increase the number of different skeletal parts that were likely to be preserved together. As Voorhies (1969:53) has pointed out, the

number of different parts is less important than their characteristics of sorting. Figure 5 shows that a single large or dense Group III bone, such as a skull, could have more paleoecologic significance than a large number of Group I bones, such as vertebrae, ribs, podials, etc. For both small animals and large, bones vary enough in relative dispersal potential so that the proportions of different dispersal groups, rather than the absolute numbers of different bones, will provide the most useful taphonomic information.

The Hydraulic Equivalence of Bones and Quartz Grains

The size of a quartz grain that is hydraulically equivalent to any given bone can be calculated by using either direct measurements of the bone's settling velocity or calculations based on the properties of size, density and shape of the bone. The

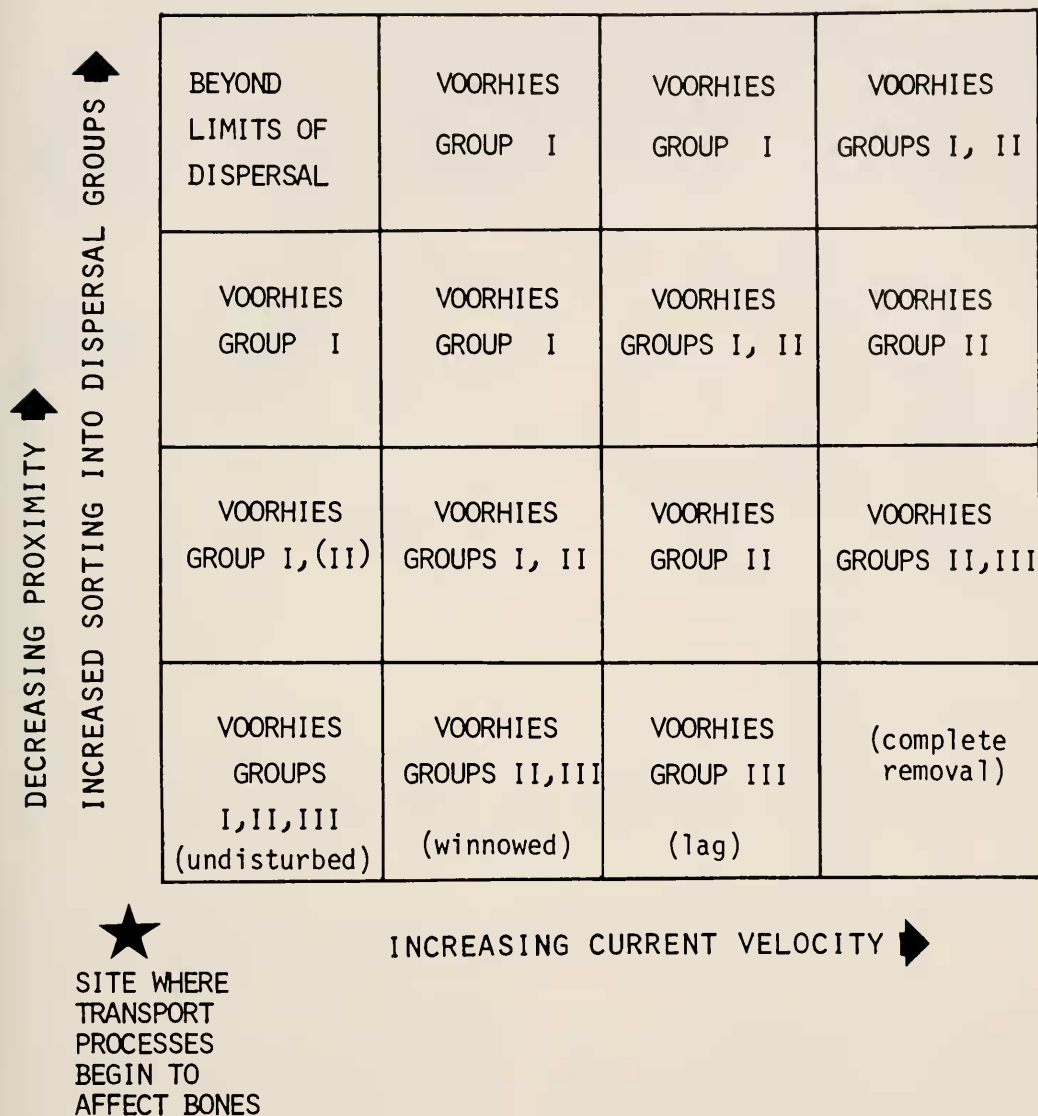


Figure 5. The formation of hypothetical dispersal groups of bones according to current velocity and proximity to the place where bones begin transport (usually the site of death). The bones included in each Voorhies Group are given in Table 2. For bones that have been disarticulated prior to transport, the three groupings on the bottom part of the chart represent the skeletal associations most "proximal" to the place of disarticulation. For fossil vertebrates, such associations can provide the most paleoecologic information on the habitats of the living animals, when examined in the context of the sedimentary environment where the bones were preserved.

equations for calculating hydraulic equivalence are given in Appendix 2. Since the shape factor is very difficult to quantify, calculations of quartz equivalence are of limited value without actual experimental

data on bone-settling velocities. A series of such experiments was conducted which provides information on the relative importance of the shape factor in affecting settling velocities.

DIAMETERS OF QUARTZ GRAINS WITH EQUIVALENT SETTLING VELOCITIES

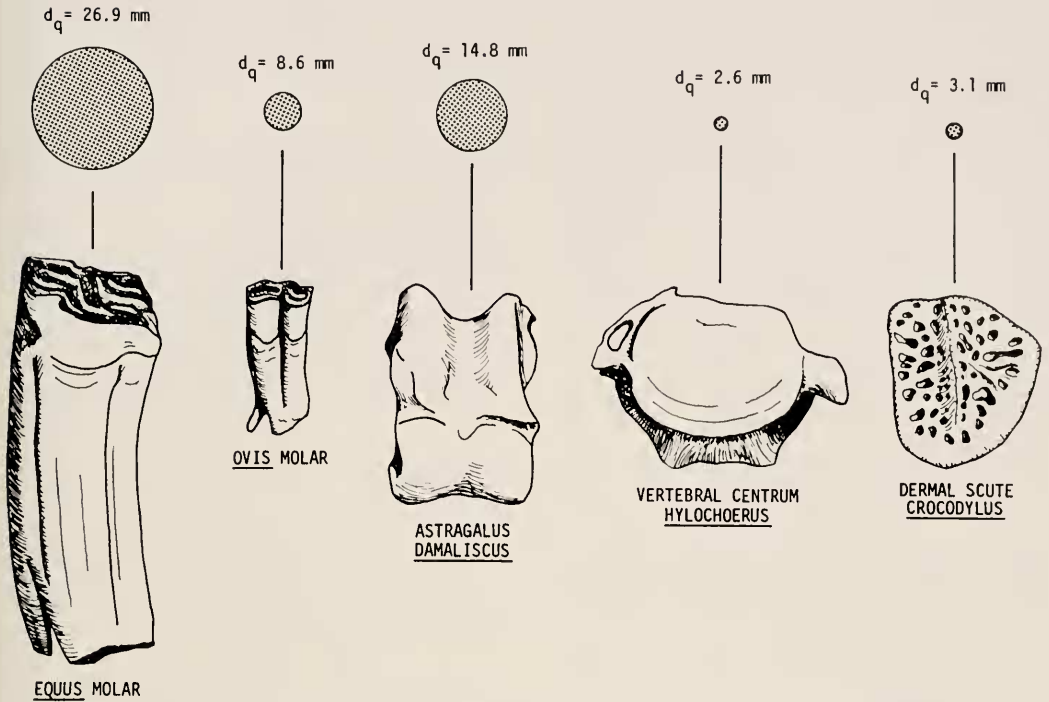


Figure 6. The hydraulic equivalents of different recent bones, as determined by settling velocity experiments. The equivalent quartz grain sizes were calculated using the method shown on Page 492 and the data given in Table 3. Density variation in the bones is the primary factor causing the variability of the hydraulically equivalent grain sizes. (Bones and grains are drawn to correct relative sizes.)

variation in bone-quartz equivalence is shown graphically in Figure 6. It is obvious that the lighter bones, such as the vertebral centrum, and bones with high surface area to volume ratios, such as the crocodile scute, will be more easily transported than the heavier and more spherical bones. The quartz equivalents agree well with the evidence for differential dispersal potentials of these bones from Voorhies' (1969) flume study. Combined evidence from the settling velocity and flume experiments provide the general background necessary for predicting the behavior of bones in transport situations. More work is needed, however, since in specific cases, the hydraulic equivalence and flume data do not agree. The sheep scapula, for instance, has a relatively large quartz equivalent (10.5 mm), which

is inconsistent with its high potential for dispersal in Voorhies Groups I/II.

THE HYDRAULIC EQUIVALENTS OF FOSSIL BONES

It would be useful to be able to predict, in general, the original quartz equivalent of any given fossil bone. Such data could then be compared with matrix grain sizes associated with the fossils. The quartz equivalent of any object can be calculated if its density and volume are known, and if shape can be disregarded or corrected for. The basic equation is:

$$d_q = (\rho_b - 1) \cdot d_b / 1.65$$

d_b = Nominal diameter of the bone = $\sqrt[3]{1.91 \times \text{Volume}}$
 ρ_b = Bone density

For bones, the crucial question is, "How important is shape in affecting the size of the quartz equivalent?" This can be clarified by comparing the actual settling velocities of bones with predicted rates based only on volume and density. Table 3 shows that most predicted settling velocities are faster than the measured rates, by an average of about 12 percent. For the lightest bones, the predictions indicate slower rates than are actually observed, with an average error of about 14 percent. The ribs and crocodile scute show a much greater difference, with predicted settling velocities exceeding the observed velocities by 33 to 74 percent.

For most bones, it will be possible to estimate quartz equivalents by using volume and density, and to estimate a possible range of error owing to the shape factor. For bones that have predicted settling velocities within ± 15 percent of the

TABLE 4. AVERAGE DENSITIES OF POROUS AND COMPACT BONES AND TEETH.

	Porous	Compact	Teeth
No. in sample	14	18	10
Mean	1.11	1.65	1.96
Range	1.01-1.29	1.36-2.00	1.70-2.24

actual settling velocities, the quartz equivalents can be estimated within about ± 25 percent. Most bone shapes will fall within this range. Although the range of possible equivalent quartz sizes is broad, it should be possible to equate bones with general grain-size groups such as coarse sand, pebbles, etc. Bones with high surface area to volume ratios, such as ribs and crocodile scutes, will have a much broader range of possible quartz equivalents, and cannot be satisfactorily approximated using the method described above.

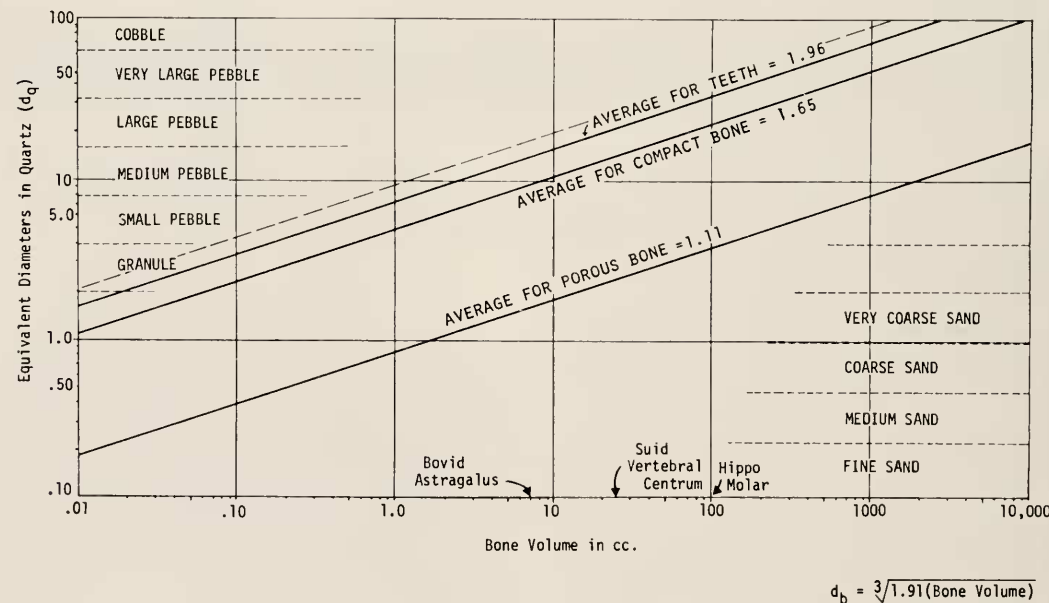


Figure 7. A log-log graph relating bone volumes to hydraulically equivalent spherical quartz grains for three average bone densities: 1.11, 1.65 and 1.96. Given the volume of any recent (or fossil) bone and a measure (or estimate) of its density, a range of hydraulic equivalents can be read off the ordinate. This estimate should be within $\pm 25\%$ of the actual quartz equivalent (d_q) for most bones, with the exception of high surface area to volume bones such as ribs. See Appendix 2 for method of calculating hydraulic equivalence (d_b = nominal diameter of bone).

Quartz equivalence gives the size of quartz grains that would settle at the same rate as a given bone. This is not necessarily the size of quartz grains that would be transported with the bone. However, settling velocities are related to transport potential, as shown by the Drag and Critical Stress formulas (Pettijohn *et al.*, 1972:335), and hydraulic equivalence provides a general idea of how bone and sediment sizes should be related if both are transported by similar processes.

For fossil bones, an important factor in calculating hydraulic equivalence lies in correctly estimating the original density. Mammalian skeletal parts are composed of three basic structural components of differing densities; porous bone, compact bone and enamel/dentine. Most whole bones include both porous and compact parts, and overall densities range between the two. It may not be possible to tell the original proportions of porous and compact bone in a fossil, but the original density should lie between the average values for each structural type. This will put upper and lower limits on predicted values for quartz equivalents.

In order to obtain representative average densities, the data given in Appendix 2 were averaged for teeth and a selection of the most porous and the most compact bones. The porous bones include patellae, vertebral centra and terminal phalanges, while the compact bones include metatarsals, distal tibiae, scapulae and ribs. These provide generalized but realistic average densities for porous and compact bones (Table 4). Using the average densities, it is possible to construct a graph relating bone volume to equivalent quartz grain sizes (Fig. 7).

Figure 7 can be used to relate fossil bones to hydraulically equivalent quartz grains in a general way. A rather low level of resolution is all that can be expected considering both the wide range of quartz diameters that are possible owing to the shape factor ($\pm 25\%$) and the problems

encountered in estimating the densities of fossil bones. However, this is enough to provide useful information. Thus, a 100 cc tooth (e.g., a large hippo molar), is theoretically equivalent to a quartz pebble between about 34 and 56 mm (nominal diameter). The tooth is within the large to very large pebble size range. A bovid astragalus of 7.0 cc, considered as a compact bone, has an estimated range of quartz equivalents between 7.3 and 12.3 mm ($9.8 \text{ mm} \pm 25\%$). The actual quartz equivalent of an astragalus of this size was measured at 9.4 mm (Table 3). Thus, Figure 7 can be used to estimate ranges of quartz equivalents possible for fossil bones (excluding ribs, scapulae, etc.), and in most cases the actual quartz equivalents will probably be close to the median of this range.

CURRENT VELOCITIES AND BONE TRANSPORT

Since bones of different sizes and densities can be related in a general way to hydraulically equivalent quartz grains, it is theoretically possible to predict what current velocities are needed to move bone particles. This can be done by using the graph of J. Allen (1965: 109) which relates current velocities to quartz grain sizes in terms of transport and deposition (Fig. 8). The scale for quartz grain size is simply converted to scales for bone grain size at each of the three average density values. Thus, it should take a flow velocity of about 80 cm/sec. to move a bovid metapodial of 100 cc (nominal diameter = 5.7 cm). To move large mammal bones (1000 cc, nominal diameter = 12.4 cm) should require flows of over 150 cm/sec.

From a theoretical standpoint, bones of the size range for most East African mammals should be transportable in flow velocities of between 10 and 150 cm/sec. Bones > 1000 cc of animals such as hippo, rhino and elephant will disperse much less readily, and only at flow velocities of > 150 cm/sec. Predictions for the transport velocities of any bone or bone assemblage

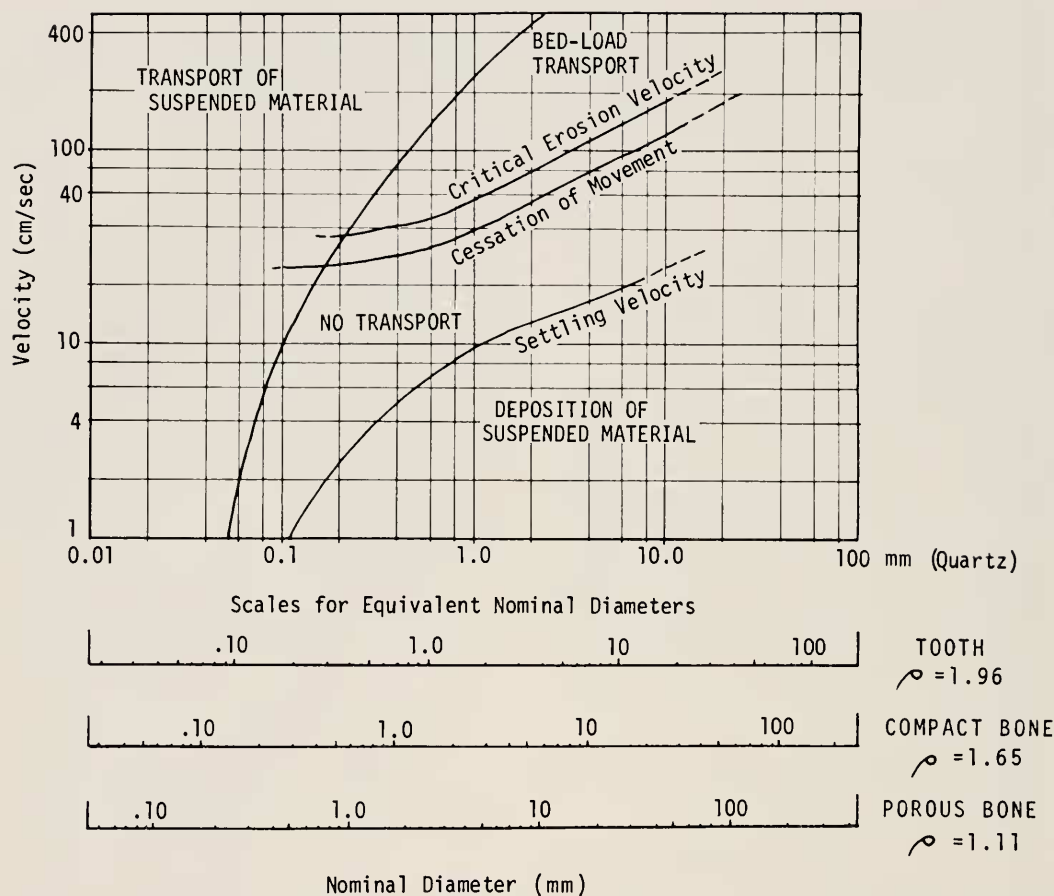


Figure 8. Theoretical transport velocities for bones, using the graph of J. Allen (1965: 109), which plots quartz grain sizes against current velocities. The three lower scales show nominal diameters of bones of three average densities. These scales give the calculated hydraulic equivalents of the quartz grain sizes shown directly above them on the abscissa of the graph. Bones and quartz grains are considered as ideal spheres. The actual shapes of bones will cause their quartz equivalents to range between about $\pm 25\%$ of the quartz equivalent for a sphere (with a broader range for ribs and other high surface area to volume bones).

are possible if volumes are known. The theoretical framework for bone transport should be tested experimentally to determine how closely predictions fit facts.²

² Allen's (1965) graph refers to the current velocity necessary to move a particular grain *on a bed of similar-sized grains*. Therefore, the analogy to bones must be restricted to those bones which are associated with a bed of clasts of similar nominal diameter (or, more precisely, on a bed of bones of similar shape and size). Preliminary flume experiments conducted in 1974 (subsequent to the completion of the above manuscript) indi-

However, until such experimentation can be carried out, the theory provides a general framework for understanding bones as sedimentary particles.

cate that bones on a bed of smaller grain size will move at lower current velocities than those predicted from Figure 8. Experiments in a natural stream show that large bones (e.g., a cow tibia) on a sand and gravel bottom may not move even at mean flow velocities of 150 cm/sec. However, in both flume and stream experiments, the Voorhies Groups for bone sorting remain valid.

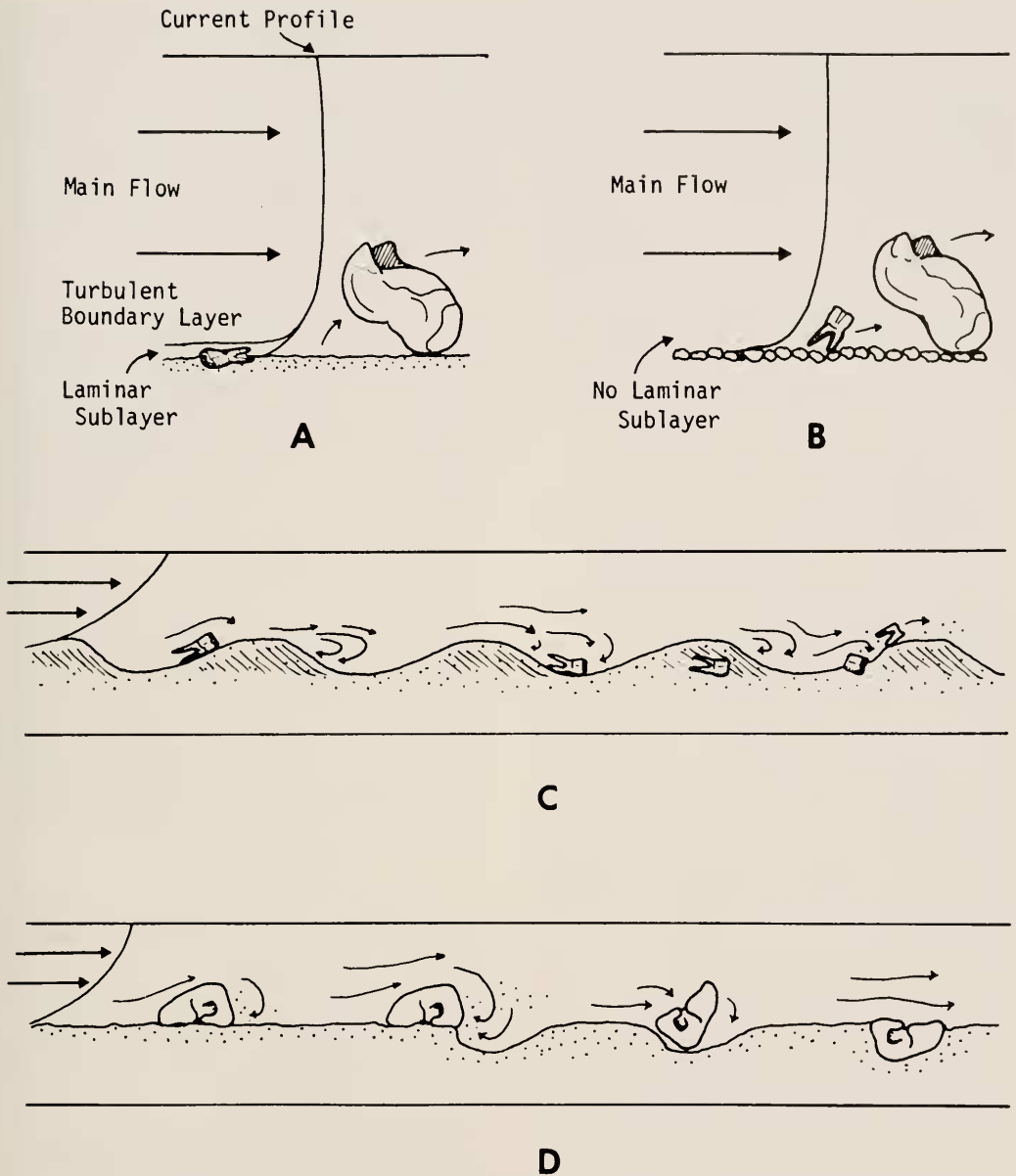


Figure 9. The effects of current profile and bottom morphology on bone transport: A, a small tooth remains at rest in the low-velocity laminar sublayer while an astragalus is moved by the turbulent boundary layer; B, on a coarser bottom with no laminar sublayer, both tooth and astragalus are transported together; C, a tooth is dropped on the downstream side of migrating ripples, buried, and re-excavated, losing its roots during the erosional period; D, a metapodial (seen end-on) creates turbulence and a scour pit, rolls into the scour pit and is buried.

Additional Factors Affecting Bone Transport in Natural Situations

Many factors can affect bone transport besides the basic parameters of size, density

and shape. These primarily concern the character of the environment where transport occurs (e.g., channels) and the nature of the fluid flow.

BOTTOM MORPHOLOGY AND CURRENT PROFILE

Stream velocities in natural situations are on the order of 20–150 cm/sec., with flood velocities reaching over 400 cm/sec. (Leopold *et al.*, 1964:167). However, these are *mean* velocities for the flow, measured at about 40 percent of the total depth above the bottom of the channel (for a channel 10 m deep, mean velocity is at about 4 m above the channel bottom). Velocities at the bottom of a channel are usually much less, and vary widely according to bottom morphology. The rate of decrease of current velocity near the base of a flow is plotted as a "current profile" (Fig. 9).

If the channel bottom is smooth, a thin, low velocity sublayer will separate turbulent flow in the main part of the channel from the sediment interface (Pettijohn *et al.*, 1972:333). Particles that are smaller than the depth of the sublayer may be left behind as lag while larger particles that penetrate into the main flow are transported. In this way, very small or flat bones and teeth could be sorted from larger bones, creating lag and transport groups that might not fit predictions based on relative settling velocities. It is possible that this had some effect on the lag behavior of jaws in Voorhies' (1969:66) experiments, since his flume had a fine-grained, smooth-surfaced bed.

If a channel bottom is rough, the turbulent boundary layer extends to the surface of the bed, and the velocity of the flow increases upward less abruptly than for smooth beds (Pettijohn *et al.*, 1972:334). Ripples and dunes or coarse sediment can cause this effect. A relatively large bone transported as part of the bed load over a smooth bottom would tend to be retarded if it encountered a rough bottom by the decrease in the velocity gradient. In areas of active dunes or ripples, the bone should have a good chance of being buried by the advancing bed forms (Fig. 9). Bones would also tend to be retarded or trapped in areas of coarser sediment such as gravel

bars. Not only does the bottom velocity decrease over gravel, but the critical boundary stress for a bone among large particles greatly increases. This is related to the "kinematic wave" effect of Langbein and Leopold (1968), in which large particles tend to concentrate other large particles during sediment transport.

FLUID DENSITY

Fluid density is generally considered to be close to 1.0. However, if it is increased by a large suspended load, then bones will be transported more easily. A high density boundary layer or a sediment-charged flow resulting from a flood can significantly increase the ability of a flow to transport bones. Sorting of bones that are less than or equal to the density of the flow would not occur since all would "float," regardless of size. This is one of the only ways to produce a completely unsorted but transported bone assemblage, where current velocity and fluid density are large enough that bones of all sizes and densities become part of the suspended load. This would be a very unusual natural transport situation.

BURIAL POTENTIAL

The more easily a bone can be buried, the less likely it is to be transported any significant distance. Bottom conditions will have an important effect. Loosely packed sand or soft mud can effectively anchor a bone, particularly if it has projecting parts. A scapula would be unstable if oriented spine-down on a hard bottom, but would be quite stable if the spine were buried in bottom sediment. This would instantly convert a Voorhies Group I/II bone to Group III "lag."

The potential for deep burial of large particles in active channels is low, even under heavy flow conditions (Leopold *et al.*, 1966:213). Low density elements such as bones would have little potential for deep burial during sediment movement un-

less covered by advancing dune or ripple fronts. Flow separation and turbulence on the leeward side of a ripple or dune is likely to trap larger particles at the base of the slip face where they can be buried (Fig. 9). As the ripple moves on, the bone may be re-excavated and carried further. Thus, progression of a bone down a channel with active bed forms would be a series of stops and starts, with a good deal of abrasion occurring during each re-excavation.

Larger bones that are beyond the carrying capacity of the flow may also move slowly along the bottom due to localized effects on the flow. A large particle on a sandy bottom creates turbulence and eddies on its leeward side which will tend to remove the sand, creating a scour pit (Leopold *et al.*, 1966). The bone could be tipped into its scour pit and buried, or a new scour pit could form, thus moving it slowly downstream (Fig. 9). A good deal of abrasion would occur during this process.

The most likely places for final burial are in the actively aggrading parts of a channel such as point bars and sand or gravel bars, or in the fill phase of scour-and-fill. Bones will move along a channel, suffering progressive abrasion, until they encounter such a situation.

Conclusions: Bones as Sedimentary Particles

A number of points can be made which are relevant to the interpretation of fossil assemblages. These are as follows:

- 1) Densities of bones soaked in water for five minutes vary from less than 1.0 to about 2.00, and teeth range from about 1.7 to 2.24. Variation in the densities of bones available for transport is high owing to differences in densities of different skeletal parts and to the presence of trapped air pockets in bones with remaining organic matter.
- 2) For mammal bones of sheep size and above, current velocities typical of

sedimentary systems can form distinct dispersal groupings of elements (Voorhies Groups). The theoretical dispersal potential of bones appears to depend primarily on density and size, with shape becoming more important for those with high surface area to volume ratios (e.g., ribs).

- 3) Close proximity of a bone assemblage to the original habitats of the living animals can be indicated by the presence of all dispersal groups in association (but disarticulated), or in some cases by the presence of lag elements. The total number of different skeletal parts in a disarticulated assemblage is not a valid measure of proximity unless these represent the full range of dispersal potentials (e.g., patellae to skulls).
- 4) Settling velocity experiments indicate that shape factors will increase or decrease bone settling rates by about 15 percent from rates predicted on the basis of density and size alone. The nominal diameters of quartz grains that are hydraulically equivalent to fossil bones can be approximated within a range of ± 25 percent (owing to the shape factor), using estimated original densities. Such approximations cannot be used for bones with high surface area to volume ratios (ribs, scapulae, etc.). Most bones of mammals smaller than hippopotamus are equivalent in settling velocity to quartz particles of sand to pebble size. An association of fine-grained sediment and relatively large bones suggests (but does not prove) that different processes may have led to their deposition (e.g., bones dropped into fine sediment by a floating carcass rather than transported along with the sediment).
- 5) Considering bone-quartz equivalent grain sizes and the standard current velocities required to transport quartz particles, it can be shown that bones

under 1000 cc should be transported by currents of from 10 to 150 cm/sec. However, in order to achieve the higher velocities in this range, mean velocities would normally have to exceed 200 cm/sec. (flood conditions). Voorhies Group I would move at normal flow velocities, but Groups II and III in general would require flood conditions for significant transport.

- 6) Bottom conditions can have significant effects on bone dispersal, with irregular, coarse-grained or loosely compacted beds tending to retard bones and decrease their transport potential. This may alter the composition of the dispersal groups.

The overall conclusion relevant to the following analysis of the East Rudolf fossil assemblages is that bones, as sedimentary particles, are particularly sensitive to *sorting* according to density and size factors. In the following pages, it should be kept in mind that the interpretations of the East Rudolf material depend on the assumption that Voorhies Groups will tend to form in natural systems because of the hydraulic effects of bone size, density and shape. Various factors discussed above may alter the compositions of the bone dispersal groups in natural systems, and the interpretations of the East Rudolf assemblages should be accepted with some caution until this assumption can be tested with experiments in natural systems.

SEDIMENTARY ENVIRONMENTS OF THE KOOBI FORA FORMATION, EAST RUDOLF

The objective of this part of the study is to characterize particular East Rudolf sedimentary environments in terms of their geology and fossil assemblages. The resulting geologic, taphonomic and biologic data will then be analyzed for paleoecologic information. This section presents a geologic background for the East Rudolf deposits followed by detailed discussions of

seven sedimentary units that were sampled for fossil content. The following two sections characterize the fossil assemblages in terms of the sorting of skeletal parts and in terms of kinds of animals represented in each of the seven units.

Geologic Setting

The East Rudolf region lies on the north-eastern side of the Lake Rudolf Basin in the northern part of the East African Rift System (Fig. 10). This part of the Rift has been tectonically and volcanically active since at least 25 million years (my.) Before Present (B.P.), when general downwarping began (Walsh and Dodson, 1969; Baker and Wohlenberg, 1971). There are no well-defined boundary faults forming a single "rift valley" in this region. Instead, Lake Rudolf lies along the axis of a broad depression containing numerous horst and graben structures of various ages. The majority of the faults are north-south and are steeply dipping to vertical. The main segment of the Rift System passes through the southern end of Lake Rudolf and east of the major part of the basin, through Lake Stephanie and north to the Red Sea.

Several cycles of faulting and vulcanism have affected the Lake Rudolf Basin during the last 3 my., and the region remains tectonically active today. The structural instability has given rise to numerous local sediment traps that have been subsequently uplifted and exposed at the surface. This activity is superimposed on the broader downwarping of the basin as a whole, which has acted as a large-scale sediment trap since the Miocene. The lake itself is shallow (~ 100 m) and the depth of sediment along the basin axis is unknown. Given the large drainage area (now a closed drainage system of 146,000 km² [Butzer, 1971a:1]), the amount of sediment accumulated since the Miocene is probably considerable.

The overall sedimentary situation, which provides for relatively rapid deposition, is ideal for fossil preservation. Throughout

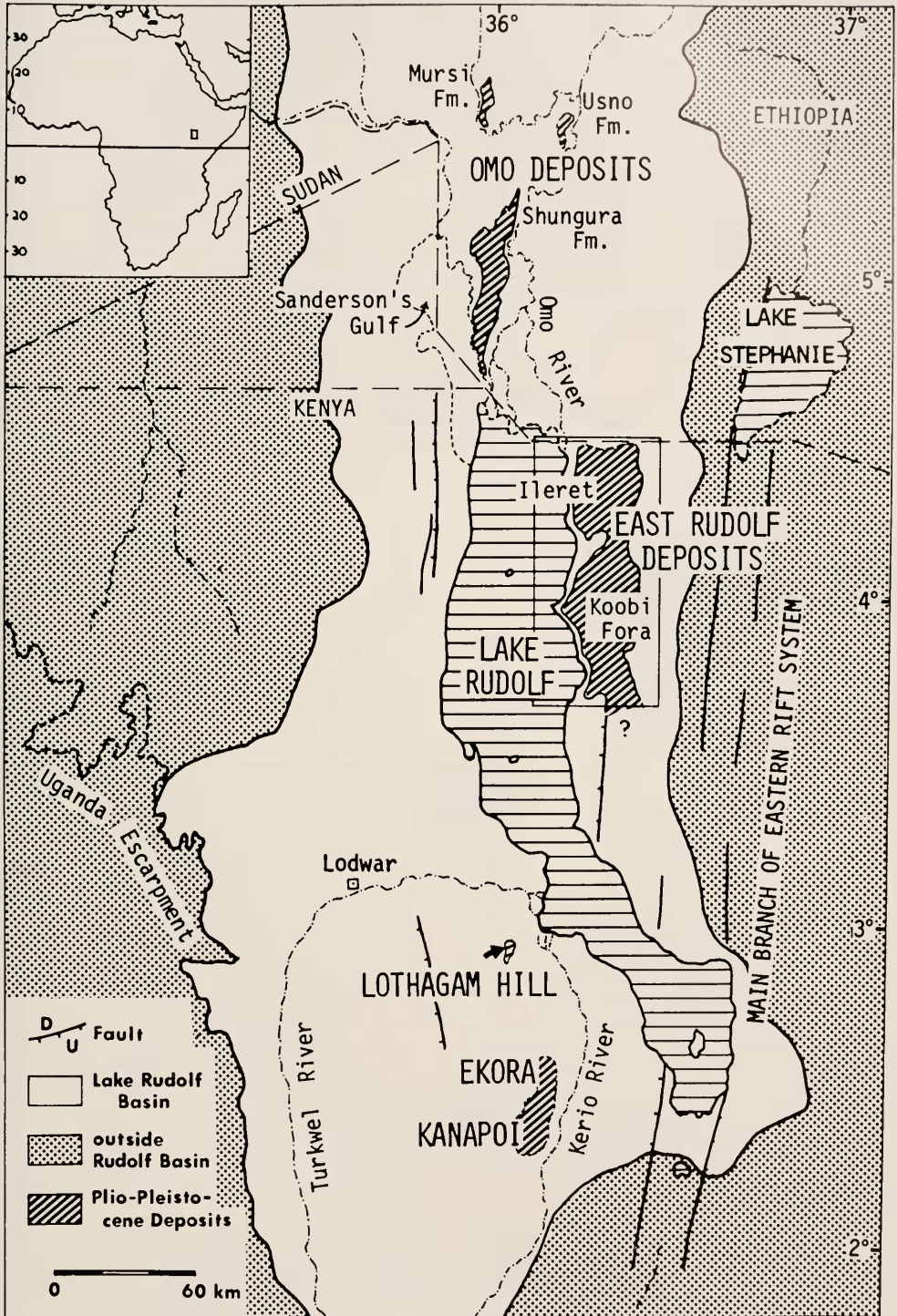


Figure 10. Map of the Lake Rudolf Basin. The area presently draining into the lake is shown in white.

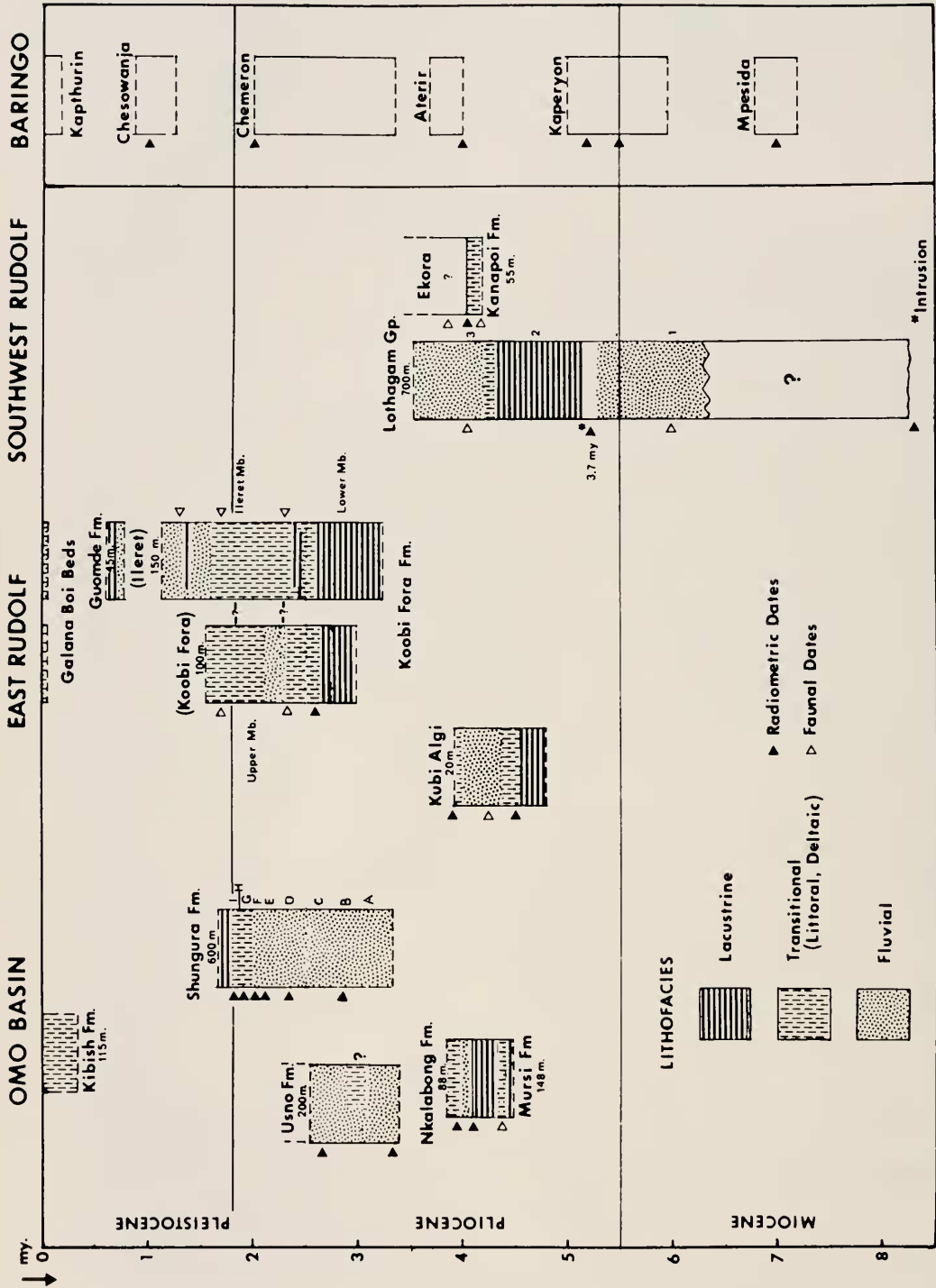


Figure 11. Correlation chart showing time-stratigraphic sequences of the Lake Rudolf Basin. Generalized lithofacies are given for each section, and their vertical range indicates the time span covered by fluvial, lacustrine or transitional deposition. The Baringo sequence, which lies to the south of the Rudolf Basin, includes several sedimentary formations of comparable age. Epoch boundary lines are drawn according to Berggren and Van Couvering, 1973, who have based their conclusions on new calibration of the type sections.

the Rift System, vertebrate fossils have been collected from various time horizons, and eventually should provide a continuous picture of faunal succession in this part of East Africa from Miocene to Recent times.

Regional Stratigraphy

Three major sedimentary deposits in the Lake Rudolf Basin are known in detail: the Omo sequence, Lothagam Hill, and East Rudolf. Extensive deposits south of Lothagam, including Kanapoi and Ekora, have provided important faunal collections and are currently under geologic investigation. These areas record periods of sedimentation for the last 5 to 8 my. in the south-western, northern and northeastern parts of the basin (Fig. 10). Correlations between areas are based on evolutionary stages of the faunas and Potassium-Argon (K/Ar) dating, with paleomagnetic reversal chronology currently showing promise as a third method. The stratigraphic relationships of the three areas are given in Figure 11. Generalized lithofacies shown in Figure 11 also demonstrate the variability of sedimentary conditions from region to region on any given time plane. For the most part, the deposits represent local conditions relating to fluctuations in base level which may or may not have been basin-wide in scale. Average rates of sediment accumulation, calculated for continuous sequences between two dated horizons, vary from 50 cm/1000 years for the Shungura Formation (Omo) to 10 cm/1000 years for parts of the Koobi Fora Formation (East Rudolf) (Behrensmeier, 1974).

The Omo Basin includes several sedimentary formations of varying ages and lithologies. Of these, the Shungura Formation (Fm.) represents the thickest continuous sequence, on the basis of radiometric age control. K/Ar dating on a succession of volcanic tuffs has provided a time scale for over 500 m of section. The Shungura Fm. has also produced a large assemblage of vertebrate fossils which can be ac-

curately placed in the stratigraphic sequence. These factors combined have made it a standard reference for faunal and time correlations between 1.7 and 3.8 my. B.P. in the Lake Rudolf Basin. The sediments represent fluvial deposition in a large-scale river system (the ancestral Omo), with a change to littoral and lacustrine deposition above "Tuff G," at about 1.9 my. B.P. (Butzer, 1971b; de Heinzelin *et al.*, 1971).

The Lothagam Group includes a thick sequence of volcanics and sediments exposed in a tilted fault block on the southwest side of Lake Rudolf. The area of exposure is only a few square kilometers, much less than for the Omo or East Rudolf sequences. Dates from a basalt flow and an intrusive sill, plus evolutionary stages of the fossil faunas, put the Lothagam sediments between about 8 and 3.5 my. B.P. Deposits of Lothagam-1 and -3 bear lithologic similarities to the Shungura Fm. and are fluvio-deltaic in origin whereas Lothagam-2 is clearly lacustrine (Patterson *et al.*, 1971).

East Rudolf covers some 5500 square kilometers (900 square miles) and its sediments represent an overall accumulation of over 300 m (Fig. 12). The oldest unit, the Kubi Algi Fm., occurs primarily in the southern part of the region. It is sparsely fossiliferous and has not been studied in detail, thus it is not discussed in this study. The Koobi Fora Fm., which forms the bulk of the fossiliferous deposits, is spread over a wide area and is extremely variable in composition, so that correlation is difficult even along continuous exposures. A K/Ar date of $2.6 \pm .26$ my. B.P. (Fitch and Miller, 1970) and paleomagnetic chronology (Brock and Isaac, 1974) indicate a time span of 3.0 to 1.4 my. for this unit.

The East Rudolf deposits are bounded on the east by Miocene volcanics, which they lap onto unconformably. The Kokoi Ridge, which divides the Ileret and Koobi Fora areas, is formed of recently uplifted Pliocene basalts with interbedded lacustrine sediments (Bowen and Vondra, 1973:391).

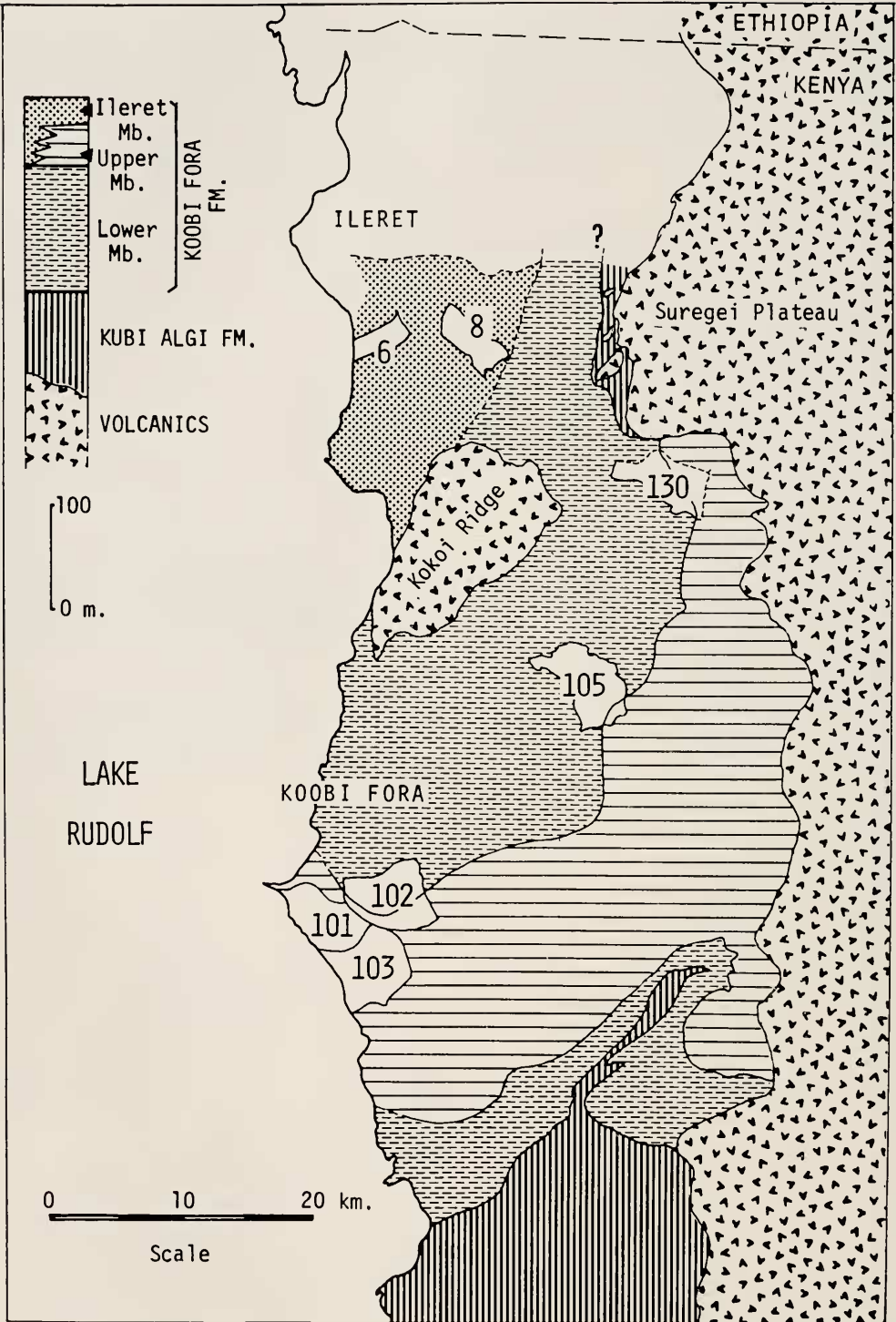


Figure 12. Generalized geologic map and stratigraphic section of East Rudolf, based on Bowen and Vondra (1973) plus unpublished work by Bowen. Numbered areas were used for controlled sampling of the vertebrate fossils which provided the material for this study.

The paleoslope, as indicated by numerous determinations of paleocurrents, inclined toward the southwest, as it does today. The Stephanie Basin probably drained across this area periodically during the Plio-Pleistocene (B. E. Bowen and C. F. Vondra, personal communication), but it is doubtful that a major river system such as the Omo River existed in the East Rudolf region. Rather, the geomorphic and sedimentary situation can be reconstructed as set of coalescing piedmont fans and deltas derived from moderate relief (about 600 m or 2000') volcanic and basement terrain toward the east. The distance from the major part of the Plio-Pleistocene lake margin deposits to the areas of highest relief (if similar to today) was on the order of 40–50 km, and the regional gradient would thus have been 600 m/50 km or about 12 m/km.

The geologic evidence indicates that this part of the Rudolf Basin contained a lake which acted as base level during the period of Plio-Pleistocene deposition. At present, it is not known whether this lake was connected to the Nile drainage during the deposition of the Koobi Fora Fm. The fossil and modern aquatic faunas (vertebrates and invertebrates) show close Nilotic affinities, and it is fairly certain that at least periodic connections have existed (Butzer *et al.*, 1972). The abundant and diverse molluscan fauna of the Koobi Fora Fm. indicates fresh water conditions. It seems likely that both closed and open drainage situations, and saline and fresh-water conditions, existed periodically during the Plio-Pleistocene in the Lake Rudolf Basin.

Recent Limnology

A summary of the recent characteristics of Lake Rudolf is useful for comparison with Plio-Pleistocene conditions. Today Lake Rudolf has a surface area of 7500 km² and a catchment area of 146,000 km² (Butzer, 1971a:1). Most of the influx of water comes from the Ethiopian Plateau via the Omo River during its seasonal

floods in July (Butzer, 1971a:37). The lake basin itself is semiarid, with about 380 mm (15") of rainfall annually (1936–1970), as measured along its shores (Butzer, 1971a). Maximum daily temperatures range from 34.0–36.0°C, and this plus the strong southeast trade winds encourages evaporation from the lake surface. The seasonal fluctuation in water level is over one meter. Longer-range fluctuations have caused the lake to drop 20 m between 1896 and 1940, and to rise 5 m in the last ten years. During the period between 9500–7500 B.P., Lake Rudolf was approximately 80 m above its present level (Butzer, 1971a:15).

The present alkalinity of the lake is .0194–0.210, and the pH about 9.5 (Beadle, 1932: 187). Ca is low in the lake water owing to the high pH, and Beadle (1932: 186) noted evidence for active precipitation of CaCO₃. Alkalinity is due to high K and Na content. The overall conditions of the lake are presently outside the tolerance of most of the molluscan forms that are typical of the Plio-Pleistocene and Holocene deposits, and only three living species have been recovered (T. Hopson, personal communication). Fish and plankton are abundant, however. Recent, apparently living stromatolite formations have been dredged up by a fisheries research vessel near South Island (T. Hopson, personal communication).

It is evident simply on faunal grounds that the lake has changed greatly since the Plio-Pleistocene, and also in the past 10,000 years. The water level has fluctuated widely, and along with it, alkalinity and pH have altered. All evidence indicates that the lake has been fresher, and the regional climate probably wetter (at least periodically), than at present.

The recent sedimentary environments associated with the Omo Delta have been examined by Butzer (1971a). These include "flood basin" (alluvial flats associated with the Omo river channel), "delta fringe" (distributary and inter-distributary flats) and the "prodeltaic zone" (subaquatic

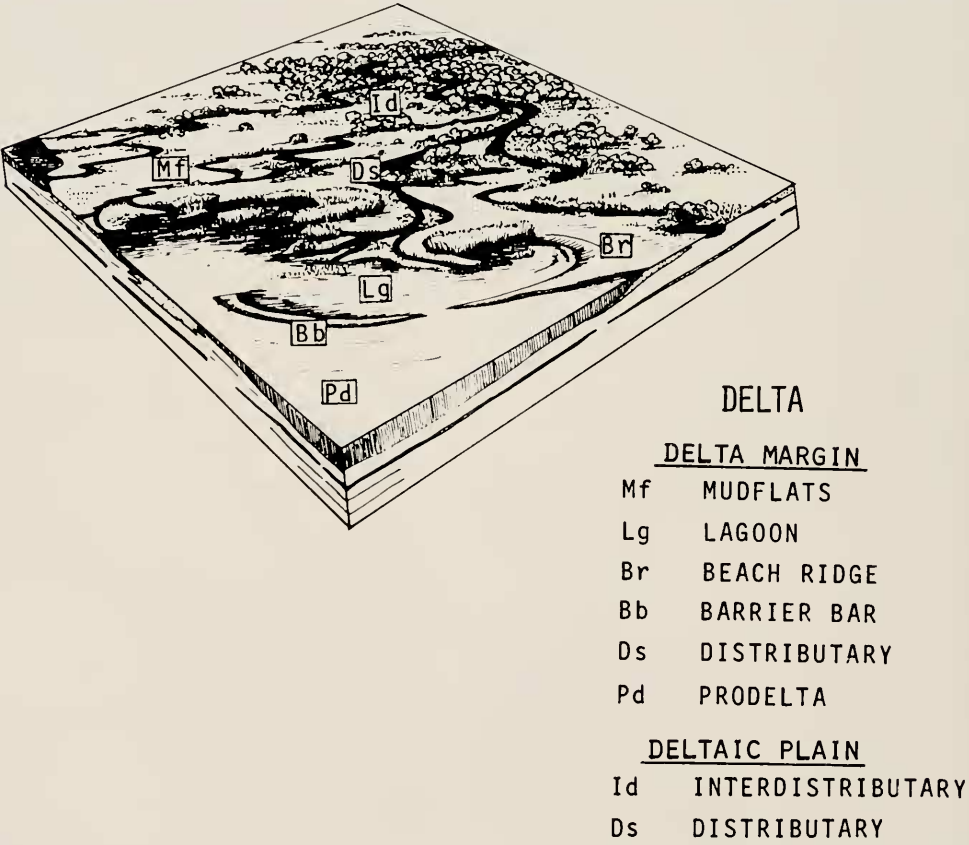
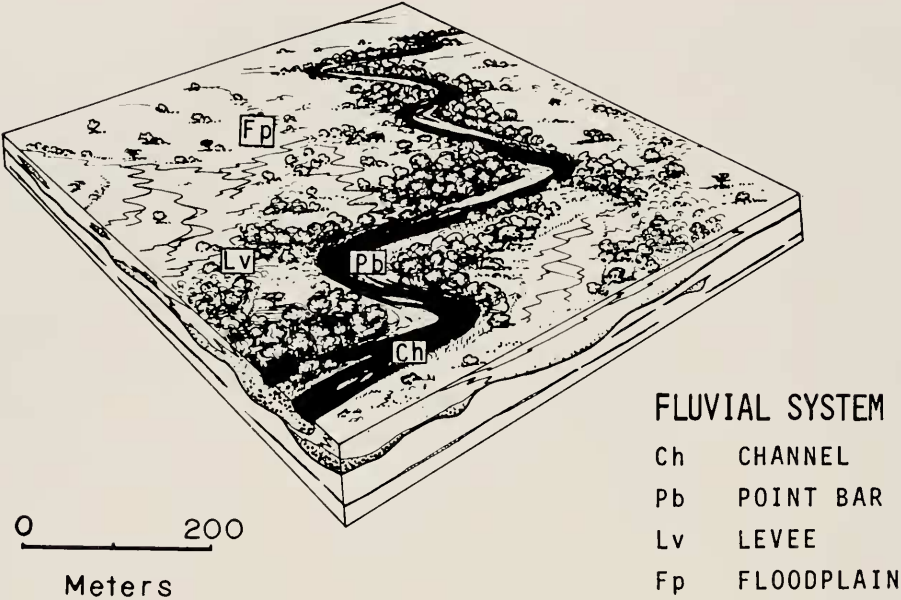


Figure 13. Diagrammatic representation of the fluvial and deltaic sedimentary environments that are recorded in the Plio-Pleistocene deposits. The diagrams are based on characters of recent fluvial and deltaic environments near the shores of Lake Rudolf.

sedimentary extension of the delta). Characteristics of these environments, including information on sediment type, vegetation, and sedimentary structures, are invaluable in interpreting the Plio-Pleistocene sediments around the Lake Rudolf Basin. Observations (by the author) of recent environments along the eastern shore of the lake, outside the Omo delta system, have also proved useful in the interpretation of the older sedimentary environments.

In order to discuss the paleoenvironments of the East Rudolf sediments, it is necessary to provide a terminology that describes the environments present in the combined lake-margin and fluvial system of the Lake Rudolf Basin. Figure 13 and Plate 4 give a verbal and pictorial description of the recent environments to be used for interpretation of the Plio-Pleistocene deposits.

Stratigraphy of the Koobi Fora Formation

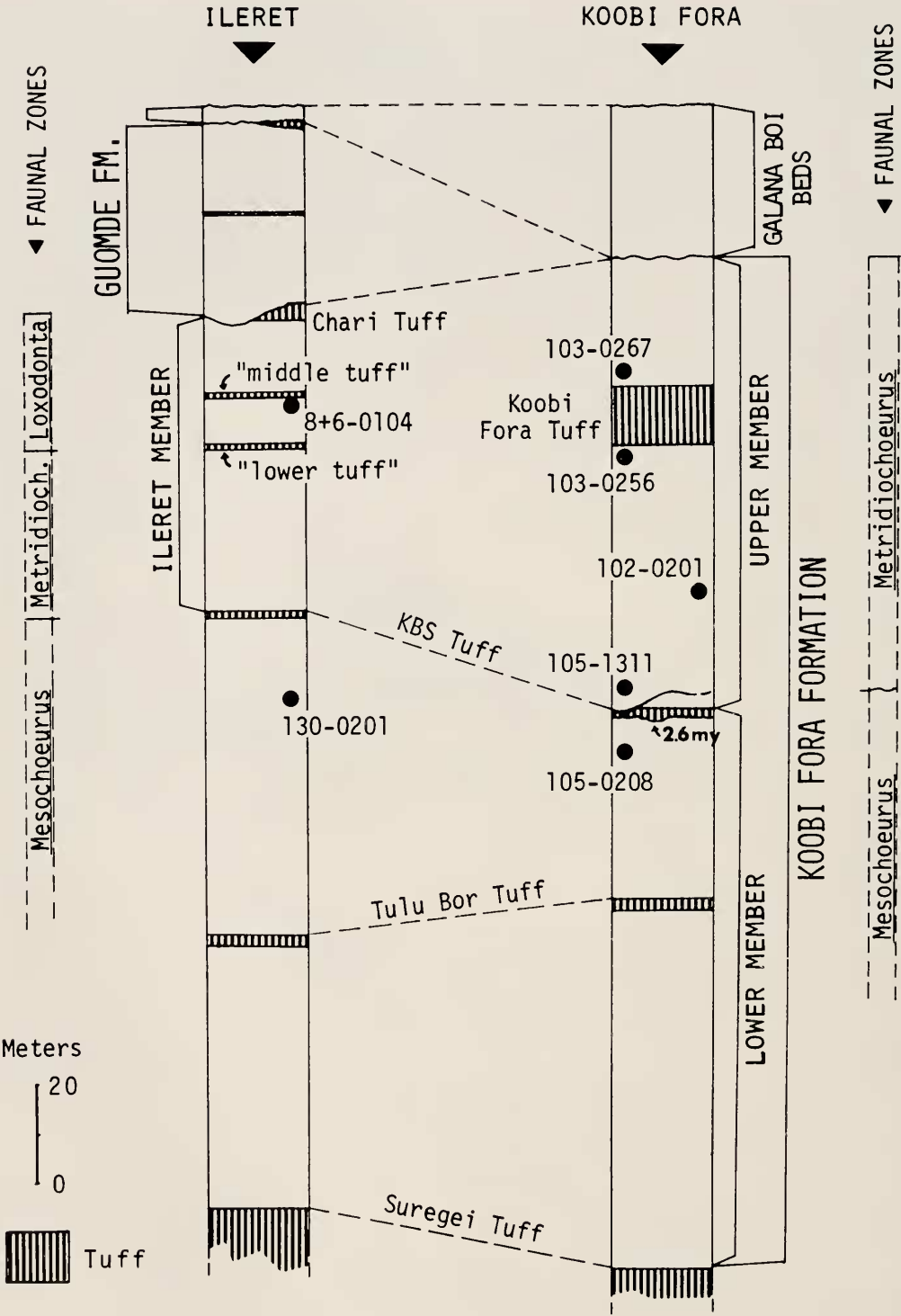
The Koobi Fora Fm. as a whole has been interpreted as a "prograding deltaic complex," with general upward coarsening indicating outward growth and thickening of the deltaic deposits through time (Bowen and Vondra, 1973:392). The paleogeography of the deltaic complex at particular time horizons has yet to be understood, but a primary lobe probably originated from the Lake Stephanie region. Sedimentary sequences in the Ileret and Koobi Fora areas are different during similar periods of time, and the Kokoi volcanics may have divided the two regions into separate depositional basins during early phases of uplift.

Stratigraphic nomenclature and sedimentary relationships have been established by Bowen and Vondra (1973). Although direct stratigraphic correlation between the discontinuous outcrops typical of East Rudolf is difficult, there are several marker horizons of reworked volcanic ash which are recognizable over much of the area covered by the Koobi Fora Fm. Three of

these tuffs, the "KBS," the "Tulu Bor" and the "Suregei," are indicated in the stratigraphic sections given in Figure 14. They lie within about 150 m of predominantly lacustrine and prodeltaic deposits. The Ileret Member (Mb.), above the KBS Tuff, includes deltaic and prodeltaic sediments that pass upward into subaerial deposits indicating floodplain or deltaic plain conditions. These are followed by an erosional unconformity overlain by the Guomde Fm., a primarily lacustrine unit of undetermined age. In the Koobi Fora region, the deltaic and lacustrine deposits which include the KBS Tuff are followed by an erosional unconformity that may be of regional significance. Fluvial deposits follow in the northeastern part of Koobi Fora, and these pass laterally into deltaic deposits toward the southwest, which is down the regional paleoslope. The Guomde Fm. is absent in the Koobi Fora region. The Holocene Galana Boi beds cap the sedimentary sections both at Ileret and Koobi Fora.

Deposits north and south of the Kokoi Ridge show increased structural deformation near the present lake shore. In the Koobi Fora region, extensive faulting occurs west of a north-south hinge-line approximately 5 km from the Koobi Fora peninsula. The Upper Member (Mb.) of the Koobi Fora Fm. also thickens toward the west at this point. There is evidence that minor tectonic events occurred in this area during the time of sedimentation of the Upper Mb. These events are represented by truncated normal faults, and at least three episodes have been recognized (G. D. Johnson, personal communication). It is likely that faulting and increased subsidence in this region have affected rates of sedimentation and, along with this, bone preservation.

With the general stratigraphic and tectonic framework of East Rudolf as a background, the following sections will deal specifically with the characteristics of the sedimentary units sampled for vertebrate fossils.



Sedimentary Environments of the Fossil Vertebrate Localities

DESIGNATION OF SAMPLING LOCALITIES

Vertebrate fossils are particularly abundant in the upper part of the Koobi Fora Fm. from just below the KBS Tuff to the top of the unit. Extensive areas of surface fossil concentrations closely associated with particular sedimentary environments provided ideal situations for bone sampling. Seven sampling localities were chosen to provide data on bone-sediment associations.

The discontinuous nature of East Rudolf exposures has led to a numerical system of outcrop "area" designation. This has been used informally by the various East Rudolf research groups. In the interest of consistency, the fossil sampling localities used for paleoecologic analysis will be coded according to this system. Each locality is thus designated by a two-part number, as follows: 103-0256; "103" indicating that the locality is in Area 103 and "0256" indicating a stratigraphic section ("02") and a bed or horizon in the section ("56").

For the purposes of this study, a locality is defined as an area of outcrop where there is a clear association between a particular lithofacies and an assemblage of vertebrate fossils. The location of each general area where sampling took place is indicated in Figure 12. Stratigraphic positions of the seven sampling localities are shown in Figures 15 and 16. Choice of sampling localities depended primarily on the nature of the fossil assemblage, and the criteria used will be explained in the chapter dealing with the fossils. An effort was made, however, to choose localities where bone was associated with a variety of lithofacies, so that assemblages from different sedimentary environments, such as channel,

lake margin and floodplain, could be compared.

METHOD OF GEOLOGIC ANALYSIS

Most of the information used for the interpretation of the fossiliferous sedimentary environments was obtained in the field. Each of the sample localities was documented by using closely spaced stratigraphic sections. Lithologic samples were collected from each section and examined later in the laboratory for specific information on sediment size and texture. In addition, lateral facies changes and overall stratigraphic context were examined and mapped in each locality.

The important criteria for distinguishing lithofacies in the Koobi Fora Fm. have been worked out over the course of several field seasons. The sample localities were specifically examined in terms of these characters, which are as follows:

- 1) Grain size and sorting
- 2) Thickness and lateral continuity of consistent lithologies
- 3) Presence and nature of clay clasts and/or reworked CaCO_3 nodules
- 4) Limonitic nodules and mottling
- 5) Primary CaCO_3 nodules and/or beds
- 6) Presence or absence of root casts
- 7) Evidence of bioturbation, particularly burrows
- 8) Cross-stratification (large- and small-scale)
- 9) Lateral persistence of well-defined,

Figure 14. The stratigraphy of East Rudolf, after Bowen and Vondra (1973). Faunal Zones as determined by Maglio (1972) are given for the Koobi Fora Fm. The Ileret Mb. is only in part the time equivalent of the Upper Mb. (see Fig. 12). The Kubi Algi Fm. continues downward from the top of the Suregei Tuff but is not included in this figure. The two-part numbers (e.g., 130-0201) designate the fossil sampling localities used for this study and show their relative stratigraphic positions.

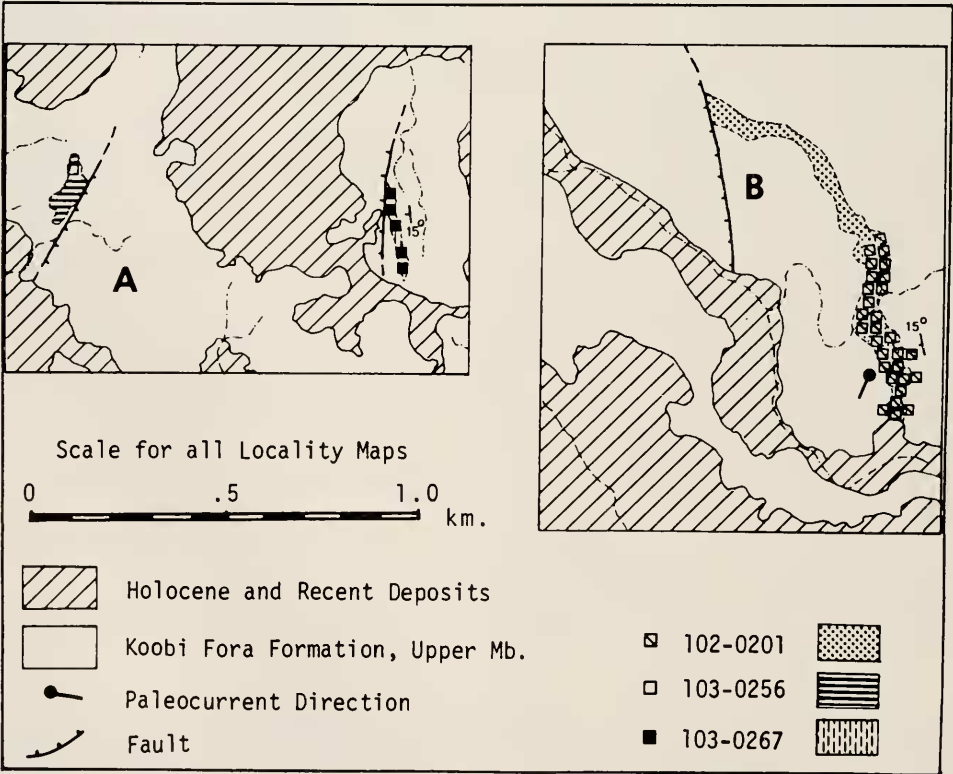
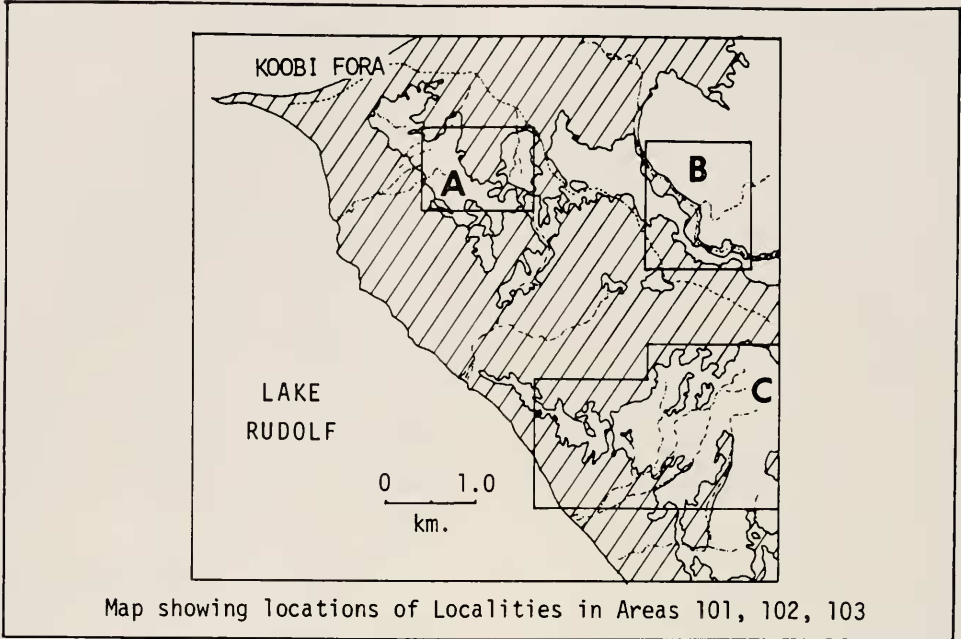


Figure 15. Maps showing the distribution of bone sampling squares (10 × 10 m) in the area near the Koobi Fora Peninsula. An index map shows the relative positions of the three more detailed maps. All maps showing square distribution are drawn to the same scale. The squares themselves are shown slightly larger than true scale.

Placement of Sample Squares in Area 103

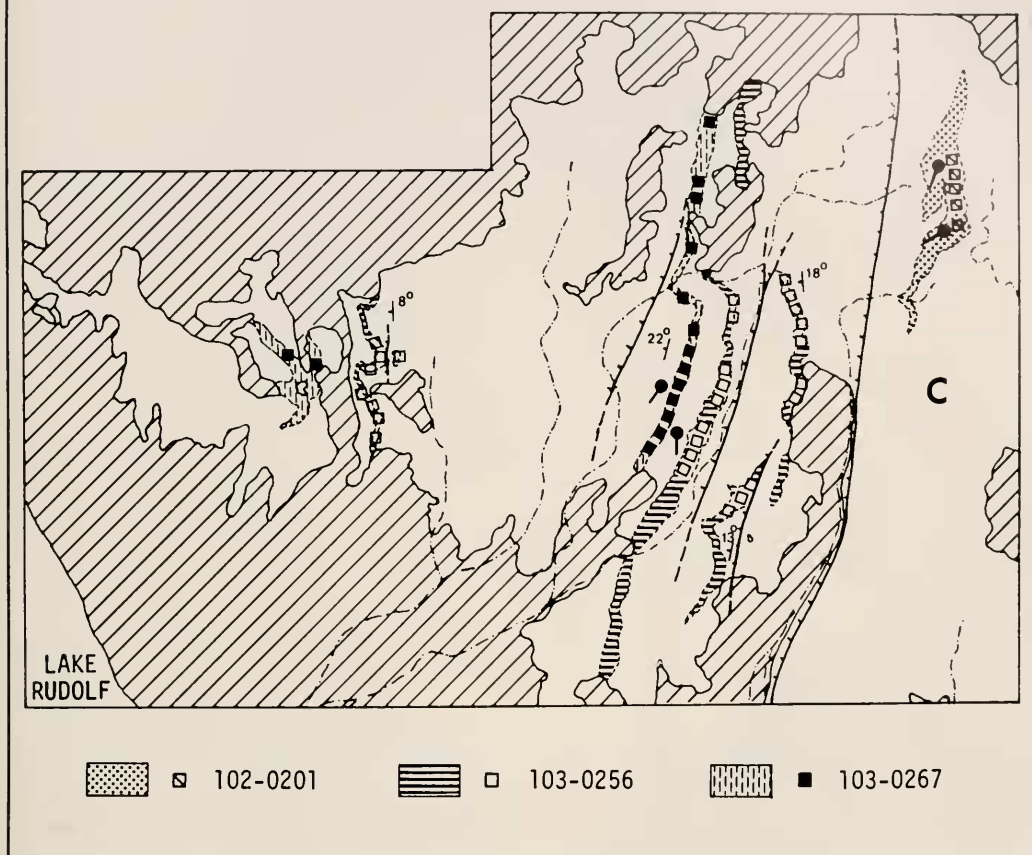


Figure 15 Continued.

even horizontal bedding and small-scale laminations

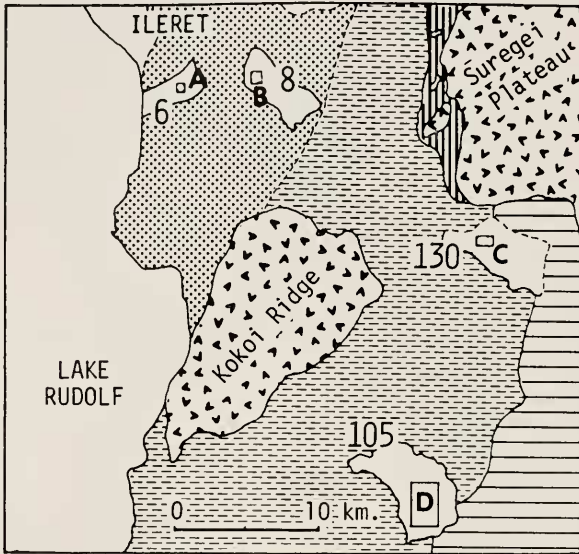
10) Desiccation structures (mudcracks)

11) Slickensides, prismatic cracking, evidence for paleosol development

12) Invertebrate fossil content

Generalized stratigraphic sections for each of the sample localities are given in Figure 17. Each locality is described in Table 5 according to the sedimentary characters outlined above, and the following

interpretations of sedimentary environments are based on this evidence. Vertebrate evidence is not included for the specific purpose of keeping this separate from other characters used in interpreting the environments of deposition. This permits the sedimentary evidence to be related to the vertebrate assemblages without danger of circular reasoning. Surface textures, hydraulic equivalents and other aspects of the bone assemblages are discussed below, after conclusions are drawn concerning each environment of deposition.



Map showing locations of Localities in Areas 6, 8, 130, 105

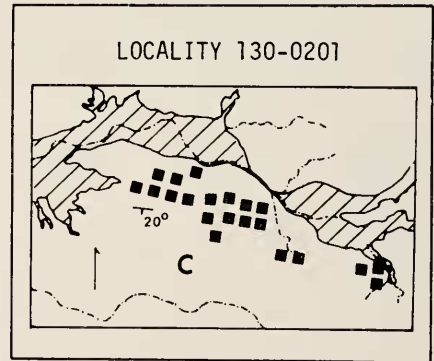
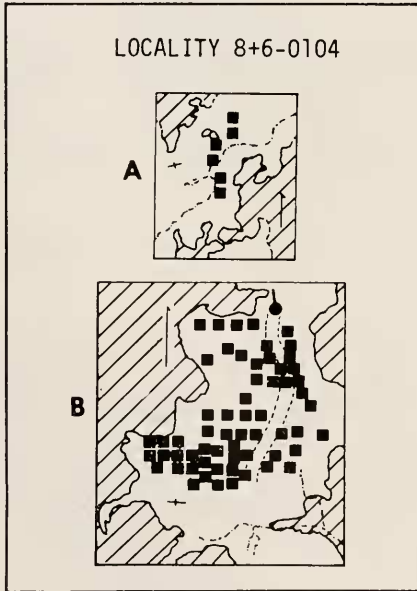


Figure 16. Maps showing the distribution of bone sampling squares (10 × 10 m) in the Ileret region and east of the Kokoi Ridge. An index map shows the relative positions of the four more detailed maps. Locality maps are drawn to the same scale as those in Figure 15, and squares are slightly larger than true scale.

Locations of sample squares in Area 105.

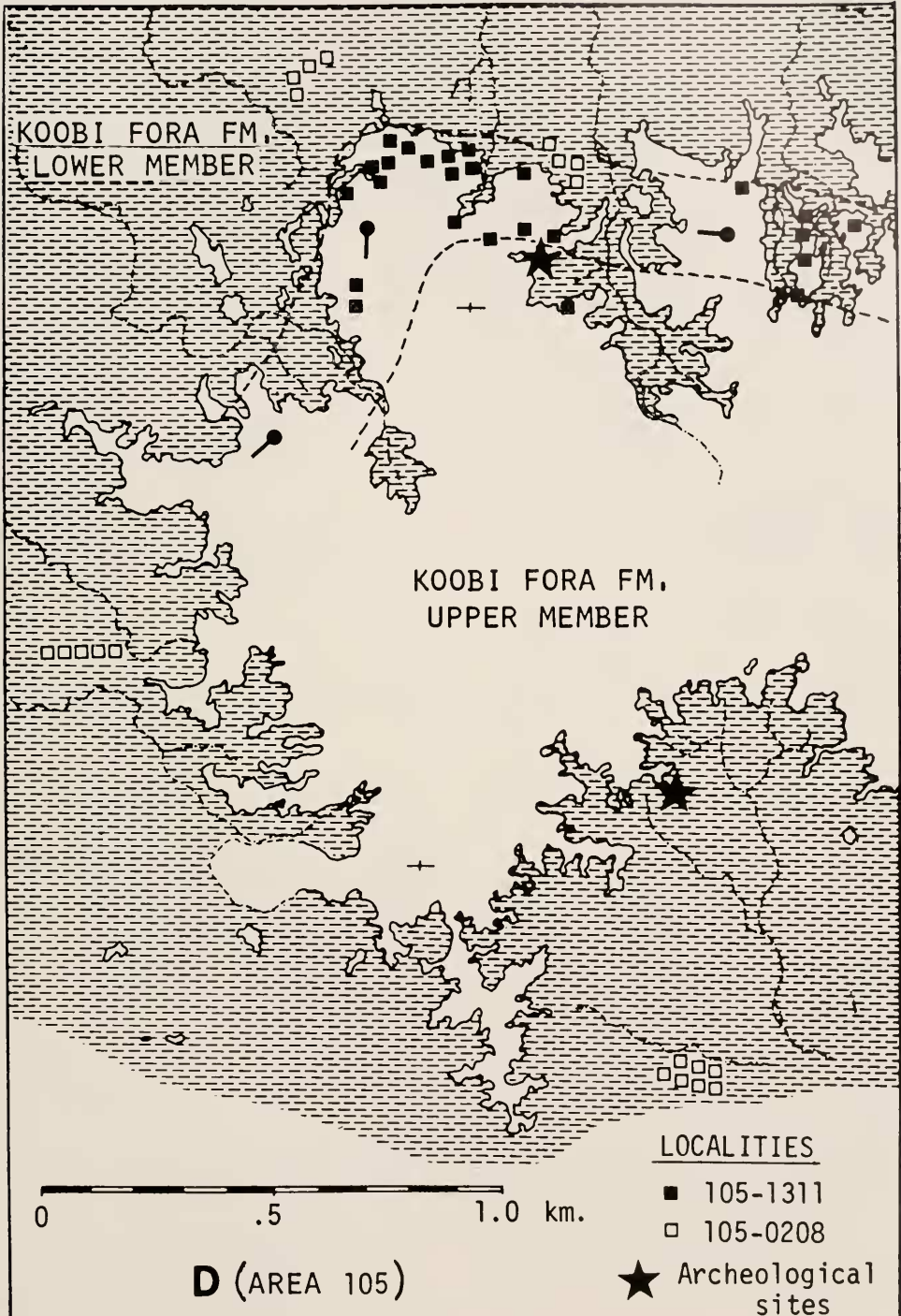


Figure 16 Continued.

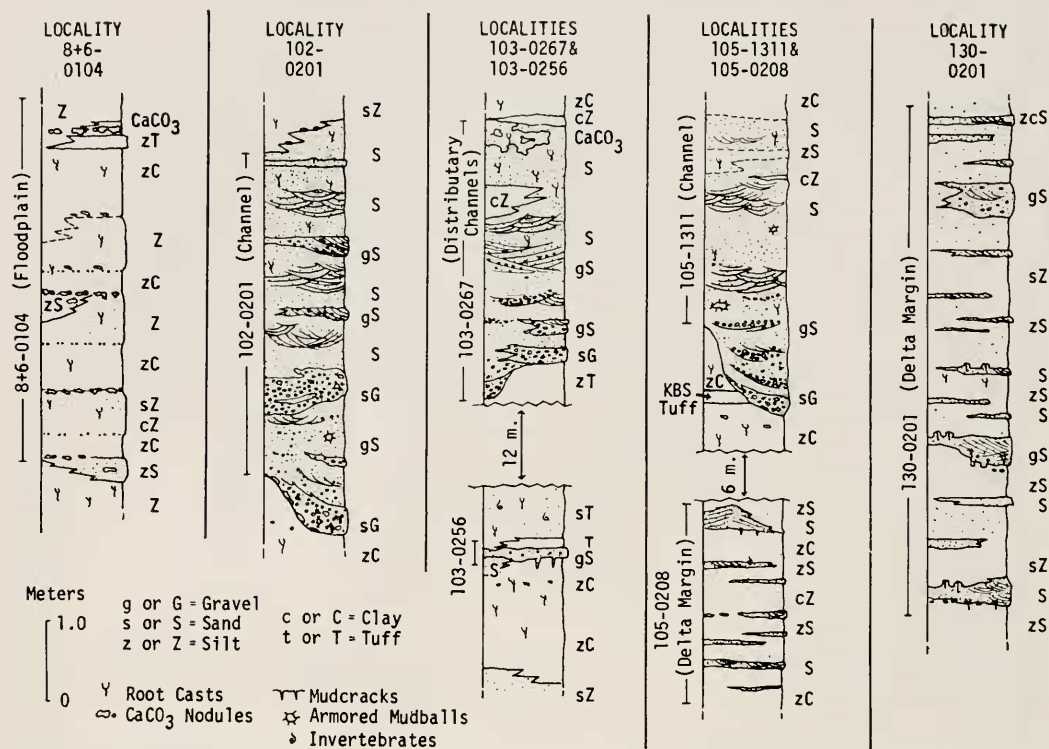


Figure 17. Detailed stratigraphic sections for each of the fossil sampling localities. The sections represent the total stratigraphic interval sampled for fossil bones, and combine the sedimentary data from many sections measured in each locality.

SEDIMENTARY ENVIRONMENTS OF THE SAMPLE LOCALITIES

Locality 103-0256: Deltaic Flats.

Most of the fossil material is derived from a thin and very extensive sand which overlies mudcracked silty clays. In the few places where the sand was not deposited, the horizon can be recognized by the mudcracked surface. There are no obvious lateral changes in the grain size of the sand unit, which is dominantly coarse to fine over the entire area. This sand is overlain by the tuffaceous silts and sands that form the base of the Koobi Fora Tuff, a 12–15 m thick unit that also covers some 2–3 km². The tuff is extensively cross-stratified in its lower part but generally is horizontally bedded with persistent horizons of mollusk shell fragments.

The sediments underlying the mud-cracked surface are much less uniform laterally and have interbedded silty clays, sandy silts and occasional lenses of coarse, clean sands. There is a general tendency toward fining from northeast to southwest, roughly following the regional paleoslope. Root casts and CaCO_3 nodules <3 cm in diameter are typical of the silty clay beds. The mudcracks on the upper surface of the unit are up to 15 cm in depth and are firm evidence for subaerial exposure. They are filled with the overlying fine to coarse grained sand.

The evidence indicates a deltaic mudflats environment of deposition for the silty clays and silts underlying the mudcracked surface. The interbedded sand lenses represent distributary channels. Bioturbation, partly due to root growth, has obscured evidence

TABLE 5. SUMMARY OF LITHOFACIES CHARACTERISTIC OF THE SEVEN LOCALITIES SAMPLED FOR FOSSIL VERTEBRATES.

FOSSIL SAMPLING LOCALITIES →	130-0201	105-0208	103-0267	103-0256	102-0201	105-1311	8+6-0104
MAJOR LITHOLOGY	silty sand	silty sand	gravelly sand	sand	gravelly sand	gravelly sand	silt
GRAIN SIZE	1-6.0 mm	.1-2 mm	.1-30 mm	.1-1.0 mm	.1-25 mm	1.0-60 mm	.1-1.0 mm
SORTING	good-poor	good-poor	good-poor	good-mod.	good-poor	poor	poor
THICKNESS	7.0 m	2.5 m	3.0 m	.75 m	5 m	3.0 m	4.5 m
EXTENT OF MAJOR LITHOLOGY	.5 km ²	2 km ²	4 km ²	2 km ²	3 km, N-S	.8 km ²	3-4 km ²
MUD CLASTS	+	+	+	+	mud balls and clasts	armored mud balls	-
REWORKED CaCO ₃	-	+	+	+	+	+	trace
LIMONITE	+	+	-	-	grain coatings	grain coatings	-
PRIMARY CaCO ₃	trace in zC	trace in zC	+	-	-	?	+
ROOT CASTS	trace	+	+	trace	+	+	+
BIOTURBATION	trace	+	+	trace	+	+	+
CROSS-STRATIFICATION	small-scale troughs in S and gS	planar fore-sets, small-scale troughs	small-large scale troughs	poorly developed small-scale troughs	small-large scale troughs, planar fore-sets	small-large scale troughs	troughs in sand lenses
HORIZONTAL BEDDING	+	+	rare	+	rare	rare	+
MUDCRACKS	-	+	-	+, on surface below sand	-	-	trace
EVIDENCE FOR PALEOSOL DEVELOPMENT	-	-	+	+, in beds below sand	-	-	+
INVERTEBRATES	-	4+ species of gastropods, bivalves in some bivalves	-	gastropods, bivalves in growth position	-	-	-
ENVIRONMENT OF DEPOSITION	Delta Margin	Delta Margin and Lagoon	Distributary Channel and Beach	Deltaic Mudflats	Channel	Channel	Floodplain

+ = observed

- = none observed

for successive land surfaces, although in some areas paleosols appear to be present (G. D. Johnson, personal communication). A laterally continuous beach sand transgressed over the deltaic flats, but apparently nowhere formed preserved beach bars or ridges. Predominantly lacustrine conditions followed, with influxes of tuffaceous material from distributary mouths and spreads of shell debris over level subaqueous surfaces.

The lack of extensive erosion on the mudflats with the coming of lacustrine conditions indicates the character of the transgression. Although the mudclasts and CaCO_3 nodules incorporated in the sand are no doubt derived from the mudflat (as are the fossil bones), the mudcracks on the surface have not been eroded away. This can only mean a very low gradient shoreline, low wave energy, and probably a relatively rapid transgression. Otherwise, it is difficult to explain why the increased energy level which carried the sand would not have formed beach ridges and eroded beach fronts, destroying the upper surface of the mudflats.

The Cretaceous Wealden Lake environment in the Anglo-Paris Basin provides some close analogues for the transgressive deposits of the Koobi Fora Fm., and particularly those of 103-0256. P. Allen (1959) reports graded sheets of pebbly sand that were spread extensively over deltaic deposits as the Wealden Lake rose. One of these, the "Top Ashdown Pebble Bed," is a graded unit with pebbly sands fining upward to sands and silts. It is only 10-20 cm thick, and truncates all underlying structures and sediments. The base is erosional, and the components of the bed are derived from underlying deposits (P. Allen, 1959:292). This is directly comparable in most characteristics to the 103-0256 transgressive sand, but differs in that 103-0256 does not appear to be derived from the underlying beds, except for the mudclasts and carbonate nodules. The base is less erosional than in the Wealden trans-

gressive sheets. The sand in 103-0256 was evidently redistributed from former beach and distributary mouth deposits and carried shoreward by the advancing lake.

The fossil bones derived from the transgressive sand and the mudflats deposits are concentrated on the slope below a strike ridge created by the westward tilted, resistant sand. They are highly mineralized, although the pore spaces of many of the fossils are not filled with cement of any kind, a unique characteristic of this assemblage. There is evidence for mixing of bones with varying degrees of predepositional weathering. Some retain fresh, uncracked and unflaked surfaces while others are weathered and have cracked or worn surfaces preserved under their sandstone matrix cover.

The quartz equivalents for the fossils, estimated according to their densities when fresh (Table 4) range from 1.0-20 mm. This is a very different size range than that of the quartz sand which forms the matrix of the fossils (<1-1.0 mm). The distributary sands associated with the mudflats contain grains up to 5 mm in diameter, yet this size range is absent from the transgressive sand and apparently was not present on the deltaic flats. If the bones were derived from the distributaries, it is reasonable to expect them to be associated with sand larger than 1.0 mm. It is possible to conclude that most of the bones were probably not brought into the area by fluvial processes, but were derived from a death assemblage that lay upon the deltaic flats. The presence of many fresh, unabraded bone surfaces further supports a locally derived fossil deposit. The bones were probably redistributed by the transgression, but final burial was evidently rapid and abrasion minimal.

Locality 130-0201: Delta Margin

Vertebrate fossils were sampled from a relatively large stratigraphic thickness (7.0 m) of tilted and faulted sediments. A variety of lithologies occur, and overall

grain sizes range from <1–6.0 mm. The dominant lithologies are evenly stratified sandy silts, silty clays and medium-grained flagstone sands. The sands are generally clean and rich in biotite. Coarser, more poorly sorted sediment occurs in laterally restricted lenses.

This locality lies within the marginal deltaic facies of the Lower Mb. of the Koobi Fora Fm. The units sampled for fossil vertebrates appear to be on an actively aggrading margin of the deltaic complex. The sedimentary characteristics listed in Table 5 agree in many respects with Butzer's (1971a:79) description of the modern Omo interdistributary basins (lagoon mudflats and marsh), including the presence of limonitic mottling in the silts and clays. The more evenly bedded and extensive silts and sands may belong to the prodeltaic zone as well. The lack of evidence for surface exposure and root-bioturbation suggests generally subaqueous conditions, with water depths greater than the maximum tolerated by aquatic vegetation (about 1–2 m).

The poorly sorted gravelly sands are restricted to lenses that represent channels. Pebbles up to 6 mm in diameter occur in these lenses as floating grains in a coarse sand matrix. Mudclasts are also present. The combined evidence suggests at least periodic currents over 100 cm/sec., and possibly flood deposition of the kind leading to the very poor sorting and large floating grains (Pettijohn, 1957:254–255). (Vertebrate bone fragments and teeth are often extremely abundant in these gravelly sands, and include a high proportion of nonaquatic forms, in contrast to the aquatic assemblages derived from laterally associated lithologies.)

Cross-stratification is often well-developed in the medium- to fine-grained sandstones. These include small-scale structures comparable to "Kappa" and "Nu" cross-stratification that indicate linguoid ripples (Fig. 18). The well-sorted medium to coarse sands show planar foresets, and in some

cases the cross-stratification suggests beach or barrier bar deposition comparable to that reported for recent barrier environments (Davies *et al.*, 1971). Current directions for the various forms of cross-stratification are highly variable. The bed forms and grain sizes indicate water movement in the lower flow regime.

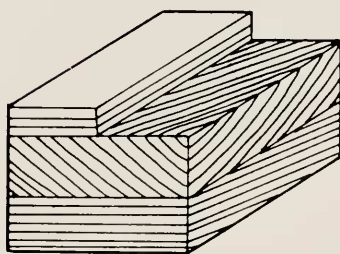
The deltaic margin interpretation of 130–0201 agrees well with the lacustrine and deltaic models of Visser (1965) for sediment types and bedding characteristics. The transgressive sand-pebble sheets of the Wealden Lake and 103–0256 are absent or poorly developed. Instead, the delta of 130–0201 appears to have been continuously aggrading into a subsiding basin, with occasional periods when sediment accumulation overtook subsidence and shallow water features (root casts, sand and gravel lenses) developed.

Hydraulic equivalents for the bones range up to 50 mm, which is much larger than the maximum size of other associated particles. However, when large aquatic animals are eliminated (e.g., hippopotamus and crocodile), the mammalian remains have an estimated maximum hydraulic equivalence of 20 mm and most are less than 10 mm. This is closer to the matrix grain size in the channel lenses. The bones that are close to being hydraulically equivalent to their matrix grains also show more evidence of abrasion and weathering. These may have been carried to the delta margin during periods of high discharge (i.e., floods), and therefore may be derived from a variety of upstream source areas.

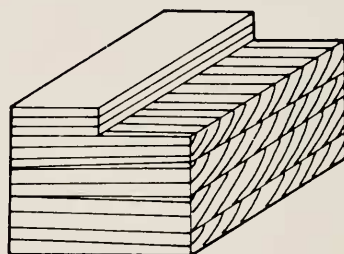
Locality 105–0208: Delta Margin and Lagoon.

The sediments are predominantly silty sands, poorly sorted and ripple-laminated with abundant mica. These form a recognizable 2–3 m thick unit over much of 105, bounded above and below by finer units of silty clays. Abundant vertebrate bone occurs in association with the silty sands but is rare in the silty clays. The silty sands

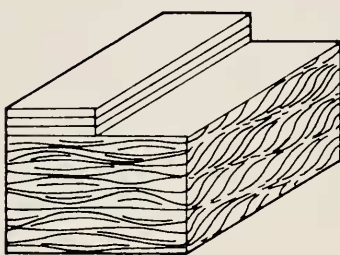
Cross-stratification typical of the sediments sampled for vertebrate fossils. (Localities in parentheses)



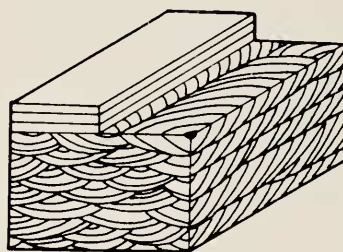
Beta-cross-stratification
(102-0201, 103-0267)



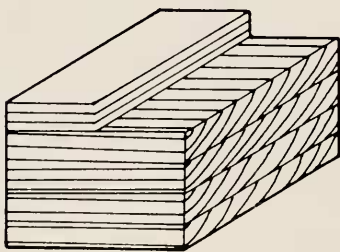
Mu-cross-stratification
(102-0201)



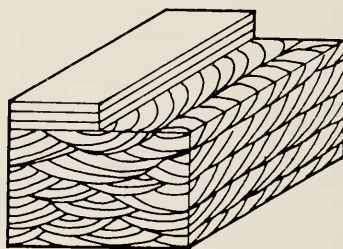
Kappa-Cross-stratification
(130-0201, 105-0208)



Nu-cross-stratification
(130-0201, 105-0208, 103-0267)



Omikron-cross-stratification
(102-0201)



Pi-cross-stratification
(102-0201)

(From J. Allen, 1963)

are characterized by horizontal, evenly bedded cosets of small-scale "Kappa" and "Nu" cross-stratification (Fig. 18). The individual beds are between 2 and 5 cm in thickness. Contorted bedding and uneven lenses of silt are present, but the bedding shows little evidence of disturbance from bioturbation. Bedding structures indicate aggradation from the advance of successive ripple fronts, such as might be expected in a prodeltaic, lagoonal environment.

Coarser sands are interbedded in discontinuous sheets and lenses. In one lens, the overall characteristics suggest a barrier or beach bar. This sand overlies the mud-cracked surface of a thin lens of silty clay, and incorporates clay clasts in its lower 10 cm. The sand body is elongate and extends for over 100 m before pinching out. Large tubular structures resembling root casts are abundant. Upward the bed becomes better sorted and has well-developed low angle planar cross-bedding that closely resembles the cross-stratification reported for barrier and beach environments (e.g., Davies *et al.*, 1971).

The more tabular, thinner sand bodies interbedded in the silty sands are commonly cross-stratified, with single sets of planar and concave-upward laminae. Shallow troughs are also common. Ripple formation at variable current velocities and depths is indicated, as in 130-0201. The sands pinch out into discontinuous nodular layers. Root casts are common, in association with the sheet sands, but mudcracks at the lower bedding contact are rare. The sands occasionally preserve a variety of fresh-water mollusks that are unbroken and locally autochthonous, including *Bellamyia*, *Cleopatra*, *Melanoides*, *Pila* and *Pseudobovaria*. The invertebrate fauna indicates "prodeltaic or even marshy" conditions (D. Van Damme, personal communication).

There are no poorly sorted, coarse-grained channel lenses within this part of the Area 105 section, in contrast to 130-0201. The overall sedimentary characteristics suggest

a lagoonal environment, with sand and silt provided from nearby distributary mouths. This compares well with delta margin conditions in actively aggrading sectors of the Omo Delta (Butzer, 1971a:75). Beach ridges and barrier bars formed at the lake-ward side of the lagoonal complex and occasionally transgressed shoreward over lagoonal sediments. The water in the lagoon probably varied in depth with shallower phases represented by coarser sand lenses with root casts indicating the spread of shoreline vegetation. The area may have been periodically (perhaps seasonally) sub-aerial, although most characteristics indicate overall shallow subaqueous conditions.

Localities 105-0208 and 130-0201 are closely comparable in stratigraphic position within the Koobi Fora Fm. Both lie near the top of the Lower Member; 105-0208 is about 8 m below the KBS Tuff, and 130-0201 between 10 and 15 m below the tuff. 130-0201 is probably the older of the two. The localities are about 15 km apart, and represent related depositional situations on the margins of the prograding delta system.

Bones of aquatic and nonaquatic animals are abundant and well preserved, and often consist of associated skeletal parts. Bone surfaces are generally fresh, with only occasional evidence of predepositional weathering and abrasion. Most of the bones of nonaquatic animals are fragmented, with spiral and saw-tooth fractures indicating predepositional breakage.

The largest bones are of hippo, and these reach hydraulic equivalents of 15-30 mm, well outside the sediment range for the coarser sands. Most of the other bone fragments and teeth are between 1.0 and 20 mm in quartz equivalent sizes. This overlaps the size range for other sediment in 105-0208, but most of the bones, and particularly the teeth, exceed 2 mm in equivalent size. Larger sediment grains occur in laterally associated facies to the east and northeast, but are absent in 105-0208. The combined evidence points to a local source of bones from the lagoon and shoreline environ-

ments, with perhaps a small component from the distributaries, including some floating carcasses. Bones were probably redistributed and buried during the migration of beach sands, a process similar in some respects to that proposed for 103-0256.

Locality 105-1311: Channel Complex.

The fossil-bearing unit is up to 4.5 m thick and overlies an erosional surface with up to 12 m of relief. Coarse gravels, including CaCO_3 nodules reworked from the underlying beds, are concentrated primarily near the base of the unit. The lithology is consistently a coarse sand with lenses of gravel. As shown in Figure 16, the main body of the sand is linear, with current directions indicating a west to southwest bend. To the south, the sands and gravels intertongue with silts and silty clays representing levee and floodplain deposition lateral to the channel.

Well-developed large scale cross-stratification is present throughout the sand unit. Troughs are the most common form and are between 20-50 cm in diameter. Gravel lenses are present at the bases of many of them. These compare well in morphology and size with "Pi" cross-stratification (Fig. 18) and with the cross-strata occurring in ephemeral streams in Central Australia (Williams, 1971). Such stratification is formed by downstream-migrating ripples of varying size in the lower flow regime (Allen, 1968:110; Williams, 1971:37).

All the above characteristics indicate that the 105-1311 sand body is a fluvial channel. The upward fining of the sands is typical of point bar formations (J. Allen, 1965:140), and it is likely that much of the sand was deposited in the point bar formed by the lateral migration of the channel bend. Root casts are abundant in the sands and laterally related silty clays, but are less common in the coarse gravels near the base of the unit. This indicates vegetation lateral to the active channels, and it is likely that a gallery forest existed along the channel. The

geologic evidence does not reveal the extent of this forest, or whether the water flow was permanent or ephemeral.

The fossil bones in 105-1311 form distinct groups according to surface texture. In one group, bones are highly rounded and polished and are less than 5 cm in diameter. They can accurately be described as "bone pebbles." These compare well with the second-cycle bones of Rief (1971), which were mineralized prior to final transport and burial. Although it is possible for bones to be thoroughly mineralized in relatively short periods of time (e.g., 5000 years for bones from Lake Rudolf Holocene deposits), the degree of rounding of the bone pebbles in 105-1311 indicates long-term abrasion. It is more likely that they were derived from earlier fossiliferous sediments associated with Miocene volcanics to the east than from floodplain deposits associated with the 105-1311 channel. The second group includes a wide range of sizes of relatively well-preserved teeth and bones. These are generally fragmental, and show signs of abrasion in their rounded edges, broken processes and exposed trabeculae. A third group consists of only a few specimens, including whole skulls collected outside the sampling areas, which show little or no weathering or abrasion. The latter two assemblages are composed of bones that had not been mineralized prior to transport, and that had undergone variable degrees of surface weathering and abrasion prior to burial. These can be referred to as "first cycle" bones.

The largest bone fragments are hydraulically equivalent to quartz particles up to 40 mm, and most of the teeth fall in the 5-25 mm range. This is well within the particle size range of the associated gravels, which range up to 60 mm in maximum diameter. A very different taphonomic situation exists in 105-1311 compared with the three localities discussed previously, which have bones that exceed the associated quartz particles in hydraulically equivalent grain sizes. It is clear that the bone as-

semblage in 105–1311 is much more likely to reflect the processes that have affected the associated sediment, i.e., abrasion and sorting through hydraulic transport. The same forces that moved sediment through the channel could also have moved the bones. A large proportion of these are probably derived from upstream sources, with a more local component derived from the undercutting and reworking of previous floodplain deposits by the laterally migrating channel. Both of these assemblages should consist of isolated teeth and the more durable parts such as ends of limb bones, all showing some degree of abrasion. The third component, consisting of the best-preserved material, would come from bones left in the immediate vicinity of the channel and rapidly buried. The bone assemblage of 105–1311 is thus a mixture of autochthonous and allochthonous material, and most of the bones show the effects of being in a fluvial system. Since the general environment of deposition is fluvial, the bones should belong to animals found in the floodplain or channel habitats, as opposed to the deltaic or lacustrine habitats.

Locality 102–0201: Channel.

The sequence is tilted some 15–20° west both in Area 102 and its continuation in Area 103. Current directions indicated in the sand are dominantly NNE to SSW, so that the strike of the beds is roughly parallel to the current. The deposits of 102–0201 overlie a scoured surface on silty clays with paleosol development, and they are followed by widespread sheet sands with stromatolites and shell debris. The stromatolites indicate shallow-water lacustrine conditions (S. Awramik, personal communication). 102–0201 represents a brief period of channel cutting between two longer lacustrine and deltaic depositional phases.

The dominant lithology is a coarse sand with gravel near the base, fining upward to medium and fine-grained sand and

finally to silt. There is no obvious trend toward downstream fining in the 3 km segment examined. Large-scale lenses of gravel up to 1.5 m thick are common in the lower 3 m of the unit. The upper 2 m have only occasional small gravel lenses and dispersed pebbles. Mudclasts and carbonate nodule clasts, which are abundant near the base of the unit, appear to be derived from the underlying silty clays. Otherwise the gravel is composed of mixed quartz, feldspar, volcanic material such as welded tuff and pieces of silicified wood, all well-rounded. There are a few polished bone pebbles and occasional large polished bone fragments indicating a source of previously mineralized material.

Cross-stratification includes planar foresets 10–25 cm in height, and a variety of trough cosets. Many cosets of the planar cross-beds are comparable to “Beta”-type stratification (Fig. 18). In some cases the cross-strata are more upwardly concave than planar, comparing well with “Mu” and “Omikron” stratification (Fig. 18). Allen (1963:110) attributes the formation of the latter types of cross-strata to migrating asymmetrical ripples. “Beta” cross-strata result from the downstream migration of single, straight edged ripple trains over a planar eroded surface (J. Allen, 1963:102). It seems that both of these conditions of ripple bedding, plus intermediates, took part in the formation of 102–0201. The troughs are generally large-scale (10–50 cm across) and compare with Allen’s “Pi” or “Nu” types of cross-stratification (Fig. 18). These are attributed to the migration of large-scale asymmetrical ripples with curved crests and projecting lobes or tongues (J. Allen, 1963:110). All of the above structures can be formed by flowing water in the lower flow regime.

The evidence is conclusively in favor of a channel origin for the 102–0201 sand. The gravel concentrations near the base represent channel bars and channel lag deposits. In one case, where the coarse material includes an unusual amount of bone, bedding

structures and local upward fining suggest point bar formation. Root casts are more common in the finer sands of the upper part of the unit than in the gravels. Vertebrate fossils show a sharp upward decrease in abundance and were clearly concentrated along with coarse sediment near the base of the channel.

The stratigraphic context of 102-0201 indicates much closer proximity to the lake than for 105-1311. In fact, 102-0201 can be regarded as a channel or complex of channels incised into a temporarily inactive delta. Evidently, base level was lowered due to either tectonic or climatic processes. The period of cut and fill separating two deltaic-lacustrine units may reflect one of the local tectonic events which affected this part of the Koobi Fora Fm. during its deposition (G. D. Johnson, personal communication).

The channel-cutting and gravels of 102-0201 may be the downstream counterpart of 105-1311. Both lie near the base of the Upper Member of the Koobi Fora Formation, and are in the *Metridiochoerus* faunal zone (Fig. 14). The composition of the gravels is similar, and some evidence for an extensive erosion surface analogous to that in Area 105 has been found in the vicinity of Area 103. If 102-0201 is the deltaic-distributary counterpart of 105-1311, then it is probably slightly earlier in time. After an erosional phase, the areas closer to base level (i.e., 102) would begin to aggrade earlier than more upland areas such as 105.

The fossil vertebrate material is variable in surface texture and overall preservation. Bones of aquatic and semiaquatic forms show minimal abrasion and are often complete. Other vertebrates are represented by teeth, limb parts, etc., usually broken and weathered. This indicates probable transport and a subaerial source (i.e., channel banks) for the bones of nonaquatic animals. A few relatively complete parts, such as a complete rhinoceros jaw, indicate closer sources and less transport.

The bone fragments are occasionally

over 50 mm (e.g., the rhinoceros jaw) in hydraulically equivalent quartz sizes. However, most are equivalent to grains less than 20 mm, and thus are similar to the size range of the gravels. As in 105-1311, most of the bone in 102-0201 has probably been subjected to winnowing and abrasion during transport. The close association between bones and gravels in 102-0201 implies similar concentrating processes. This may be an example of Langbein and Leopold's "kinematic wave" effect (1968), where large particles tend to concentrate other large particles and form gravel bars.

The sediment particles, including bones, are a mixture of allochthonous and autochthonous material. The more complete skeletal parts, the mudclasts and the armored mudballs, are examples of locally derived material from the channel banks or channel bed. The gravels, including the polished bone fragments, have been transported from upstream sources. The largest proportion of bones and teeth may have either local or distant sources, and probably represent animals which inhabited channel and floodplain environments as well as the temporarily dry and emergent deltaic plain.

Locality 103-0267: Distributary complex.

The fossil-bearing horizon is exposed in widely separated areas covering over four square kilometers. The dominant lithology is a poorly sorted gravelly sand. The sands are of variable thickness and occasionally cut several meters into the underlying beds. Coarse sediment fines upward and inter-tongues with silts and silty clays near the top of the unit.

The 103-0267 sands and gravels overlie the Koobi Fora Tuff, which is predominantly lacustrine in origin and is capped by a widespread, oolitic carbonate sand with stromatolites. The deposits of 103-0267 are followed by lacustrine silts and shell beds. Thus, the channeling and sand deposition represent a brief period of subaerial exposure and erosion similar to that of 102-

0201. About 50 m of continuous section separates the two units. G. D. Johnson (personal communication) has suggested that a tectonic event may be responsible for 103-0267 as well as 102-0201.

The upper part of 103-0267 is occasionally characterized by a discontinuous horizon of CaCO_3 concentration with abundant root casts. The root casts are truncated by the overlying sediment. CaCO_3 layers are formed of linked, irregular nodules which become more massive upward. This layer appears to bear a primary relationship to the associated sediments; i.e., it formed at the time when the top of 103-0267 was a land surface. The carbonate layer is thus tentatively identified as a caliche. It is comparable in structure and form to caliches of the American Southwest (Reeves, 1970; Aristarain, 1962; Bretz and Horberg, 1949). Although the processes leading to caliche formation are not well known, seasonal upward and downward percolation of ground water is usually indicated by such carbonate concentrations in soil horizons (Reeves, 1970: 353).

Cross-stratification is more widely variable in scale than in the 105-1311 or 102-0201 channels. The largest sets are up to 20 m across and are broadly concave upward. They compare with "Pi" cross-stratification (Fig. 18) and "festoon" bedding of the mega-ripple zone (Visher, 1965:47). A variety of smaller scale cross-stratifications are also present, including "Beta" and "Nu" types (Fig. 18). Troughs are well developed in sandy gravels near the base of the unit, while the festoon bedding occurs near the middle in coarse sands with gravel lenses.

Characteristics of 103-0267 suggest a distributary complex, with some redistribution of sediment by shoreline processes. Current directions are highly variable, from NW to S. The deposits represent laterally extensive channel cut and fill with subsequent aggradation over emergent deltaic flats. The large-scale cross-strata indicate distributary channels with flow depths of several meters. This contrasts with the

channels in 105-1311 and 102-0201, which lack cross-stratification of comparable scale and probably carried shallower flows.

The bones of 103-0267 are concentrated in the lower 3 m, and are usually associated with pebbles of about 1 cm in diameter. Large-scale gravel and bone concentrations such as in 102-0201 are absent and bones are more or less evenly dispersed over the area covered by the deposit. There is a mixture of bone surface textures indicating various kinds of weathering and abrasion before burial. Parts of aquatic animals are generally the best preserved. Second cycle "bone pebbles" are present, as in the channel deposits of 102-0201 and 105-1311.

Grain size equivalents for the bones range up to 30 mm in diameter, but most fall between 5-15 mm. Since grain sizes in the gravels are up to 30 mm, the bones are within the overall sediment size range. Many have been transported, and the assemblage includes both autochthonous and allochthonous bones, as in the 102-0201 and 105-1311 channels.

Locality 8+6-0104: Floodplain.

This unit is composed of lithofacies unique to the upper part of the Koobi Fora Fm., occurring only in the Ileret Mb. and in the Upper Mb. in Areas 130 and 131 (Fig. 12). The dominant lithology is a light-colored tuffaceous silt. The environment of deposition evidently extended over a wide area, and the silts are exposed in Areas 6 and 8, which are some 2.5 km apart. The unit is stratigraphically marked by the "middle tuff complex," which includes locally discontinuous lenses of reworked volcanic ash and pumice.

The silts are remarkably consistent in texture and appearance. They are interbedded at regular intervals with zones of silty clays. These show vertical prismatic structure and clay concentrations suggesting paleosol development. Zones of CaCO_3 nodules occur within the silts and at contacts of silty clays on silts or sandy silts. The nodule horizons are often laterally continu-

ous and formed of elongate or flattened, irregular carbonate concentrations. Internally these are composed of fine sand floating in structureless micrite. They vary in size from 2–15 cm maximum diameter. Smaller nodules of CaCO_3 are dispersed throughout the clays and silts. The sediments themselves have very little dispersed carbonate, and do not react to the HCL test. Fragments of nodules are incorporated in sand lenses representing small channels interbedded in the silts. In some cases the nodule horizons are truncated by later beds. The combined evidence leads to the conclusion that the carbonate concentrations formed during the deposition of 8+6-0104.

The nodule horizons can best be explained as incipient caliches or carbonate concentrations formed in the "B" soil zones of successive subaerial deposits. Lobova (1967:290–299) describes the formation of similar carbonate concentrations in desert soils of the USSR. He suggests they are formed by biogenic carbonate concentrated in water percolating downward from the surface which later evaporates, leaving CaCO_3 precipitates. These nodule horizons commonly form at depths of 20–60 cm below the surface. The presence of such horizons in primary association with the sediments of 8+6-0104 indicates seasonal fluctuations of water content in soils with a local (biogenic?) source of $\text{CO}_3^{=}$ and a source of Ca^{++} (clays²). The absence of extensive, thicker caliches is perhaps due to the steady aggradation of the floodplain, with continued burial of former land surfaces.

Root casts are abundant throughout the unit. They are usually less than 1 cm in diameter and are formed of CaCO_3 similar to that found in the nodule horizons. CaCO_3 -filled root casts are also found in the desert soils of the USSR, and are used as evidence of biogenic formation of carbonate concentrations (Lobova, 1967: 290). Some of the root casts are truncated by the channel scour-and-fill structures. The silts are riddled with tubes which may

be burrows rather than root holes. These are usually 1.5 mm in diameter and have distinctive clay rims.

One well-developed channel can be traced NNW across the exposures in Area 8. It is approximately 40 m across and is filled with medium- to coarse-grained sand plus pumice cobbles up to 10 cm in diameter. Some of the silt beds (and perhaps the Area 8 lens of "middle tuff") represent levee and overbank deposits from this channel. Other channels occur within the silts and clays. Most are small scale, with variable current directions. The channel sands are often well sorted and cemented with CaCO_3 , and in some cases the cemented sands weather out as rounded, resistant blocks and nodules.

It would be difficult to assign 8+6-0104 to any environment other than a floodplain. In general, the characteristics fit Allen's (1965) concept of vertically accreting flood-basin deposits. The whole complex of small channels and silt deposits may represent a zone intermediate between deltaic fan and floodplain, similar to that 1 to 2 km east of the margin of the present-day Tulu Bor Delta at Ileret. In Area 6, the "middle tuff" forms a widespread, mudcracked surface indicating deposition in a pond or lagoon, with later desiccation. It is possible that more deltaic conditions existed farther to the west of Area 8 in Area 6.

The bones of 8+6-0104 are generally very well preserved and often covered with a CaCO_3 crust. Some show surface weathering and cracking, and there are abundant isolated teeth. Associated skeletal parts of terrestrial mammals are also fairly common. This evidence suggests variable degrees of surface weathering and rates of burial.

The bones in 8+6-0104 are associated with much smaller grain sizes than in the channels. Hydraulic equivalents of most of the bones fall well above the 1 mm maximum grain size of the silts and sandy silts in which they occur. If individual bones had been carried in the channels and spread over the floodplain during floods, then they

should be found in association with grains closer to their hydraulic equivalents, i.e., coarser sand and gravel. Sediment of this size is available in channels lateral to the silt deposits. Since it is not found with the bones, and since these show a general lack of abrasion, most of the bones are probably autochthonous to the floodplain environment. The presence of associated skeletal parts may indicate carcasses buried *in situ* or floated in during the floods. Most of the bones probably were buried by the periodic influxes of floodstage silts. The trapping effect of floodplain vegetation may have been influential in anchoring the bones until they could be buried. Some of the lighter elements may have been dispersed by these floods, but most of the thanatocoenose remained in place as a lag deposit to be covered, or destroyed by later weathering.

DISCUSSION AND CONCLUSIONS

The seven localities can be grouped into three broad categories on the basis of similarities in lithofacies:

- 1) Delta: 103-0256, 130-0201, 105-0208, (103-0267)
- 2) Channel: 102-0201, 105-1311, (103-0267)
- 3) Floodplain: 8+6-0104

These groupings are similar in lithology, bedding structures, and lateral facies relationships. The deltaic localities are more diverse in these characteristics than the channels, with 103-0256 representing a transgressive beach, 130-0201 distributaries and a delta margin, and 105-0208 a beach and lagoon complex. 103-0267 can also be regarded as deltaic, since it represents a distributary complex rather than a single, well-defined channel. However, its lithology and sedimentary structures are more like those of the channels. Hence, it is intermediate between the deltaic and channel groupings, and is included parenthetically in both.

If the composition of the bone assemblages is linked to sedimentary processes, then the channel assemblages should be more like other channel assemblages than like floodplain or deltaic assemblages. The characteristics that should be similar within similar deposits include the degree of bone-sorting and the degree of weathering and abrasion. In the extreme case, the depositional processes could sort and partially destroy a given thanatocoenose so as to obscure all of the original ecological information in the assemblage.

Thus, the first step in recovering ecological information from East Rudolf assemblages is to isolate those cases where the effects of depositional processes are minimal. The evidence presented so far against extensive alteration of a thanatocoenose by sedimentary processes includes:

- 1) Bones with fresh, unabraded surfaces
- 2) Complete bones, skulls with teeth and delicate structures intact
- 3) Associated skeletal parts (indicating lack of reworking)

On these criteria, the assemblages of Localities 103-0256, 105-0208 and 8+6-0104 have been least affected by depositional processes, and retain a maximum amount of paleoecologic information. The other localities have assemblages with mixed histories, and ecological information may be more difficult to isolate.

Fossil assemblages from the channel environments (including 103-0267) are similar in that they all bear evidence for bone abrasion and include mixed autochthonous and allochthonous material. The lacustrine-deltaic environments are less similar among themselves, with Locality 130-0201 combining the characteristics of transported and nontransported assemblages, while the others appear primarily untransported. In general, however, it appears that some aspects of the bone assemblages are similar in similar lithologies, and thus reflect the processes operating in the different sedimentary environments.

SORTING IN BONE ASSEMBLAGES OF THE KOOBI FORA FORMATION

The primary object of this section is to establish the relative numbers of different skeletal parts in the seven bone assemblages and to discuss their taphonomic implications. Different skeletal parts have very different potentials for dispersal, as discussed in the section on bones as sedimentary particles. Depositional processes operating on bones should affect the ratios of skeletal parts, particularly those that have widely different densities, such as teeth and vertebrae or phalanges. Assemblages that have a concentration of elements with similar dispersal potential indicate sorting of the original components of the thanatocoenose. Assemblages with a mixture of heavy and light, large and small bones indicate either less alteration of the thanatocoenose before burial, or a mixture of bones with different taphonomic histories.

Most skeletons are incomplete when their parts become sedimentary particles, due primarily to destruction by carnivores. The initial assemblage, after carnivore activity (such as in East Africa today), consists of teeth, skulls, horn cores, vertebrae and limb ends, with more parts surviving for large animals than small. This results in an assemblage of bones with a wide range of sizes and densities, which will be subject to sorting in transport situations. The bones and teeth also have different survival potentials in most situations, with the former being more readily destroyed by taphonomic processes than the latter.

Sampling of Bone Assemblages

Most of the fossil vertebrates of the East Rudolf deposits occur in surface lag concentrations due to the removal of surrounding sediment. In general, movement of fossils away from their source rocks is minimal, and they remain in clear association with particular sediments. Conditions of preservation and recent erosion are such

that even delicate fossils usually remain reasonably intact, once exposed, and compact objects such as teeth may last for long periods of time (100+ years?) on the surface. This provides a large amount of accessible material for collection.

Bones from the seven localities described in the previous section were collected using the following procedure: Grid squares of 10×10 m were laid out over the chosen area of outcrop. The first square in each locality was positioned using an arbitrary spot on an aerial photograph or simply by selecting a local landmark (e.g., a tree or conspicuous outcrop), without specific reference to the degree of surface bone concentration. Subsequent squares were measured off from the first, with a minimum of 20 m between squares. On horizontal strata, the squares were laid out on an orthogonal 30×30 m grid. On dipping strata, the squares were positioned along the strike of the units being sampled. The grid system was adjusted, where necessary, to avoid patches of recent sediment and vegetation. The selection of squares was *not* adjusted to sample particularly attractive patches of bone fragments, in order to prevent subjective biasing of the bone samples. Collecting was done by systematically traversing a square first east-west, then north-south (for a square oriented NSEW). All the surface bone larger than 5 cm (maximum length) was collected in addition to those smaller bones that could be identified to class (Fish, Mammal, Reptile, Bird). During the first field season all samples were removed for identification and study. During the second season, after workers were familiarized with the vertebrate taxa and skeletal parts, it was possible to do most identification in the field. This greatly simplified the logistics of the sampling, and enabled workers to leave the field with a card for each square recording taxa and skeletal elements plus geological data. This was a welcome alternative to carrying out 50–60 lbs. of fossil bone fragments after each day of collecting.

TABLE 6. STRATIGRAPHIC DATA AND SAMPLE SIZE OF THE SEVEN FOSSIL SAMPLING LOCALITIES. SAMPLE SQUARES ARE 10×10 METERS, REPRESENTING 100 m^2 EACH.

SAMPLING LOCALITY	# OF SAMPLE SQUARES	STRATIGRAPHIC INTERVAL SAMPLED (IN METERS)	BASIC LITHOLOGY	GENERAL DEPOSITIONAL ENVIRONMENT	KOObi FORA FM. FAUNAL UNIT	STRATIGRAPHIC UNIT
130-0201	21	7.0	Sand, silt, and clay	Delta margin	<u>Mesochorus</u>	Lower Mb., Koobi Fora Fm.
105-0208	20	2.5	Sand, silt, and clay	Delta margin and lagoon	<u>Mesochorus</u>	Lower Mb., Koobi Fora Fm.
103-0267	20	3.0	Sand and gravel	Distributary-beach complex	<u>Metridiochorus</u>	Upper Mb., Koobi Fora Fm.
103-0256	27	.75	Sand	Transgression over deltaic mudflats	<u>Metridiochorus</u>	Upper Mb., Koobi Fora Fm.
102-0201	34	5.0	Sand and gravel	Channel	<u>Metridiochorus</u>	Upper Mb., Koobi Fora Fm.
105-1311	25	3.0	Sand and gravel	Channel	<u>Metridiochorus</u>	Upper Mb., Koobi Fora Fm.
8+6-0104	66	4.5	Silt	Floodplain	<u>Loxodonta</u>	Ileret Mb., Koobi Fora Fm.

Maps of each locality showing the positioning of the sample squares are given in Figures 15 and 16, and the number of squares collected in each locality is given in Table 6. The major problems encountered in the sampling were: 1) choosing localities that showed a clear relationship between the surface bones and the sedimentary units, 2) obtaining comparable samples from each locality that adequately represented the bone assemblages.

CHOOSING THE SAMPLE AREAS

The primary goal was to collect an assemblage of bones that represented the material buried in a well-defined sedimentary deposit. In selecting the sampling localities, the following guidelines were established:

- 1) A locality was chosen on beds, or a series of beds, representing deposition in one of three broad environmental categories: channel, floodplain or delta.
- 2) The topographic situation was such that contamination of the fossil concentrations with material from other horizons was minimal. Efforts were made, for example, to sample beds on drainage divides rather than in valleys.

- 3) Vegetation and recent sediment in the area were minimal.
- 4) Previous collecting in the area was minimal, or collection sites were marked and the removed fossils recorded.
- 5) The locality was extensive enough so that a representative sample of the fossil assemblage could be collected.

Fortunately, the East Rudolf region provided many areas that satisfactorily met all these requirements. Since stratigraphic series of environmentally related beds rather than single beds were used, the chances of contamination from different series of beds representing different depositional environments was greatly reduced. In the course of sampling, the actual bone-producing beds were often indicated by matrix adhering to fossils, and some of the samples could be assigned to particular horizons. Such evidence further supported the association of bones with the environmental units of interest.

The advantage of sampling different lithologies that are genetically related (e.g., sands, silts, and clays, all deposited in deltaic conditions) is that this will give a more general picture of the faunal and skeletal elements preserved in a rather broadly defined environment. This con-

trasts with sampling a particular bed (as in some quarry deposits), which is more likely to be the result of very local or special conditions. The sampling method described above allows coverage of extensive areas (square kilometers) of outcrops representing single, broadly defined sedimentary environments. This permits sampling on a scale more comparable to the habitat sizes of many East African vertebrates (on the order of square kilometers to thousands of square kilometers). Sampling by widely spaced squares should establish faunal and bone abundances that represent broad-scale differences between sedimentary environments and the habitats associated with them. Moreover, sampling through several meters of sedimentary strata representing extended periods of time should reveal more general pictures of bone and sediment associations than assemblages representing single events.

SAMPLE SIZE

Surface bones are so abundant in the sampling localities that even a few 10×10 meter squares provided large numbers of fragments, and over 9,000 were collected in the total sample from 213 squares. More than 7,000 (78%) of these were identifiable as to skeletal part or vertebrate group or both. Very few of the sample squares lacked fossil material, even though they were laid out without regard to fossil distribution.

The abundance of fossil material was sufficient to provide an average of 34 identifiable pieces per square and to give a good representation of the most common parts and animals. Field collecting was aimed at obtaining the largest possible comparative samples from all the localities. Since the surface concentration of bone varied from locality to locality, the number of squares collected in each varied as well. Thus, it was necessary to collect over 60 squares for 8+6-0104, which had a low surface concentration, but only 20 for 105-

0201. At least 20 squares ($= 2000 \text{ m}^2$) were collected in each locality.

Method of Representing Fossil Abundance

It is possible to represent the relative abundance of different bones in more than one way. For instance, within each locality the total number of fragments identifiable as vertebrae can be compared with the total number of tooth fragments. Percentage representations of these totals can be compared between localities. Alternatively, the total number of *squares* with vertebrae can be compared with the total number of squares with teeth, etc. For reasons described below, the second method of representing relative abundance is used in all the following analyses of the fossil assemblages.

Difficulties in using total numbers of parts for comparative purposes include the following:

- 1) One tooth, for instance, can weather on the surface into dozens of fragments which are still identifiable as teeth, but a vertebra may only produce a few fragments that can definitely be identified as vertebrae. In both cases the numbers of broken fragments, if totaled, would count for more than the whole elements, and give erroneous data on the relative numbers of these elements. This problem is particularly pertinent to a fragmented surface sample, and is almost impossible to correct for by attempting to calculate the "minimum numbers" of fragments per bone in the manner of Shotwell (1955).
- 2) A single skeleton, if disassociated prior to burial or during recent erosion, may be counted as several individuals of the same animal group, while the whole skeleton would be counted as one individual. This can lead to errors in representing the actual abundance of different animals. Shotwell's method of using mini-

mum numbers of individuals³ helped to resolve this problem for his quarry samples (1955). In the East Rudolf surface assemblages, with many vertebrate groups represented by a wide range of identifiable bone fragments, the minimum numbers method was not feasible.

The more satisfactory method of representing bone abundance for the East Rudolf localities is to use the number of squares with a particular skeletal part. This is done as follows: if one vertebra, or several, or dozens of pieces of the same one, occur in a sample square, this is counted as 1 occurrence. If one tooth of the same taxon occurs in each of 5 squares, this is counted as 5 occurrences. The number of occurrences of each bone can be converted into a "square frequency" by dividing by the total number of squares in each locality. Thus, 5 occurrences out of a sample of 20 squares gives a frequency of .25 or 25%.

This method has a number of advantages which make it a valid measure of bone abundance in the broadly defined sedimentary units of interest for this study:

- 1) It gives a measure of the *dispersed* abundance of the different bones in space and time, which should be a result of the *overall* conditions of each sedimentary environment.
- 2) The problems encountered in using fragment totals are essentially eliminated, since using occurrences in squares will greatly reduce the effects of differential identifiability and fragmentation of the surface bones. Also, since the squares are widely spaced, the probability of sampling parts of the same bone or even of the same animal more than once is very low.

A comparison of the two measures of abundance, by fragment number and by

squares, illustrates the advantages of the latter method. In Figure 19, the frequency of vertebrae in each locality is given according to total numbers of fragments identifiable as vertebra, and by the frequency in terms of squares with vertebrae. Numbers of vertebral fragments that are high relative to the square frequencies, as in 8+6-0104, imply localized concentrations. In fact, for 8+6-0104 the large number of vertebrae results from two associated partial skeletons of bovids. In contrast, a high square frequency and a low fragment number shows a widely dispersed sample of isolated vertebrae, as in 103-0256 and 103-0267, where only one or two vertebrae occur per square. The representation of the dispersed abundance is more useful in comparing bone assemblages that result from interrelated processes in channel, floodplain or deltaic environments. The "square frequency" of bones (= the number of squares with a particular bone or taxon divided by the total number of squares per locality) will thus be used in the following sections.

Characteristics of the Bone Assemblages

During the collecting of the bone sample, and prior to numerical analysis, it was apparent that some parts, such as teeth, were more abundant in some localities than others. However, most of the differences in bone proportions among the localities became apparent only after relative abundances were tabulated in the laboratory.

The bone sample contains abundant skeletal fragments from mammals, reptiles and fish, and a few from birds. Analysis of bone frequencies is restricted mainly to the mammals, which form the largest and most diverse component of the sample. Frequencies of the skeletal parts are given in Table 7. Discussion of the method of identification, which can influence the apparent abundance of parts, will precede analysis of the data.

³ The relative abundance of different taxa is represented by the number of the most common similar skeletal part (e.g., left femora) of each taxon (Shotwell, 1955:331).

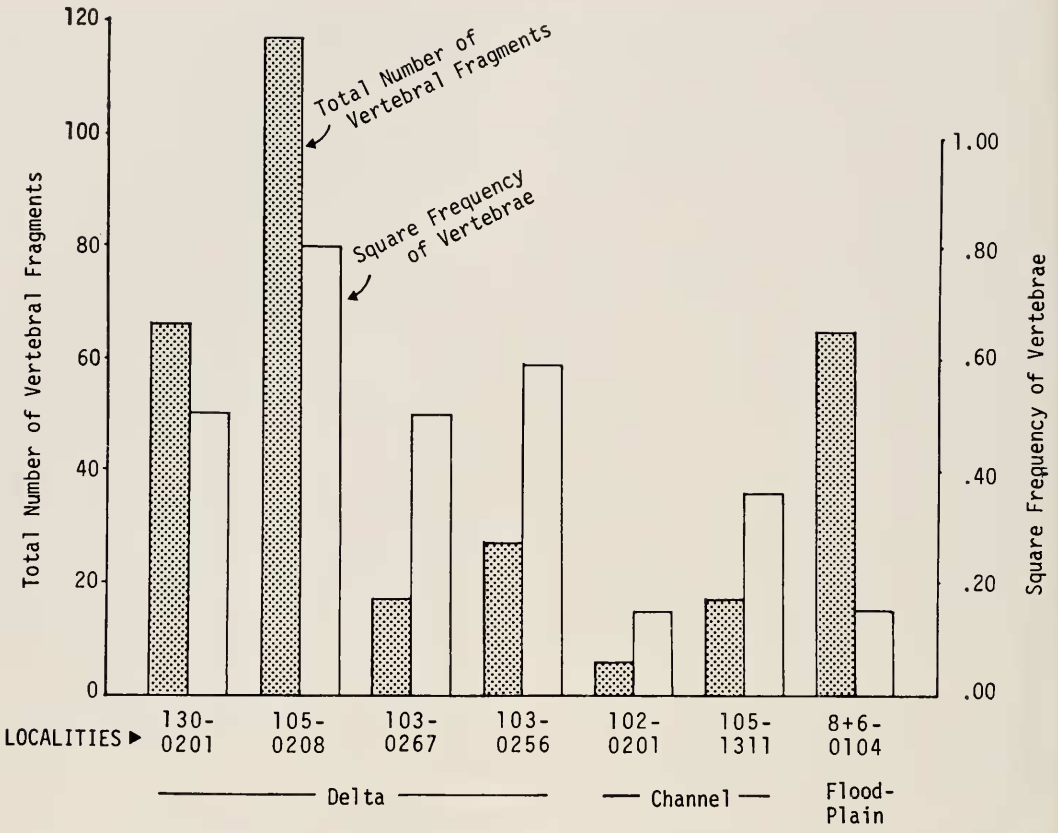


Figure 19. A comparison of two ways to represent the abundance of vertebrae in the fossil samples. The shaded bars on the histogram represent the total number of vertebrae and vertebral fragments from each locality. The white bars represent the square frequency of vertebrae, the proportion of squares in each locality which contained at least one vertebral part. Localities with a large number of fragments in proportion to the square frequency generally have associated vertebral columns (e.g., 105-0208, 8+6-0104). Localities with high square frequencies but low numbers of fragments indicate wide dispersal of vertebrae.

IDENTIFICATION OF BONES

A large proportion of the collection was identifiable as to skeletal part. For reptiles and mammals, 24 categories include all the identifiable bones. Mammals have 19 categories which can be assigned to a specific class with certainty (Table 7). Rib and diaphysis fragments, plus some phalangeal, vertebral and pelvic fragments, cannot always be assigned to class. These are not included in the frequencies for either mammals or reptiles.

The number of identifiable fragments of different bones is variable and can lead to

a bias for greater apparent abundance of the bones with more identifiable parts. However, since all the bone fragments were identified in a consistent manner by one person (A.K.B.), there should be little or no effect on the locality to locality comparisons. There will be some effect on the absolute abundance of certain elements within each locality. Teeth, for example, are always more identifiable than other parts and thus will appear to have higher frequencies than is actually the case. The use of "square frequency" helps to minimize this effect, since only squares with at least one partial tooth (excluding fragments of

dentine or enamel) were counted. Differences in the numbers of identifiable fragments of other bones, particularly for mammals, probably have an insignificant effect on their relative "square frequencies" in this study. Most bones were represented in each square by at least one relatively complete part (e.g., ends of limb bones, vertebral centra, whole phalanges, etc.).

SIGNIFICANCE OF THE FREQUENCY DATA

The data given in Table 7 show that most of the skeletal parts are represented in each locality. Some have consistently high frequencies, such as teeth; some low, such as patellae, and some are variable. The lower frequencies indicate occurrence in only a few squares out of the total for each locality. Both high and low frequencies are of interest in comparing the samples.

To assess the statistical significance of the frequencies, one must ask, "How representative of the actual bone assemblage in each locality are the 'square frequencies'?" In some respects the problem is comparable to establishing binomial sampling limits for accurately detecting character frequencies in any given population (Simpson *et al.*, 1960:199). In such cases, tables are available for relating actual frequencies to observed frequencies using various sample sizes. For example, a character with 40% frequency in the actual population could vary from 12–35 occurrences in a sample of 60, with a probability of only .001 that fewer than 12 or greater than 35 occurrences would be observed.

The binomial sampling limits for square frequencies can be calculated using the Harvard Tables (1955). For a sample of 34 squares, a frequency of .32 (11 squares) could represent a possible range of actual frequencies between .17 and .48, with a probability of only $p = .05$ that the actual frequencies in the bone assemblage would fall outside of this range. The sampling error indicated by simple binomial probability is potentially rather large. However, it can be assumed that the square fre-

quencies are more closely representative of the true bone frequencies because: 1), each sample square consists of a 10×10 m area, which greatly increases the probability of finding a particular bone if it is present in the assemblage and 2), many squares include more than one bone of a particular kind, and the actual frequency is higher in these cases than representation by square frequency would indicate. Therefore, the square frequencies will be treated as representative frequencies for the following data analysis. The bone abundances, as represented by these frequencies, should be comparable from locality to locality. The statistical significance of specific differences or similarities between localities was tested using Chi-Square analysis.

COMPARISONS OF OVERALL BONE CONCENTRATIONS

The relative concentration of identifiable bones varies greatly in the sample squares of the seven localities. Overall bone abundance can be conveniently expressed by dividing the cumulative total of bone occurrences in squares by the number of squares in each locality. These figures are given for identifiable mammal and reptile parts in Table 7. Locality 8+6-0104 has the lowest concentration and 105-0208 the highest. The three channel assemblages are no more concentrated than the lacustrine-deltaic ones for mammals, but are slightly less prolific in terms of reptiles. There does not appear to be any consistent correlation between sediment grain sizes and identifiable bone abundance in the deposits sampled.

The localities with more bones per square do not appear to have more of any particular elements. Rather, they show an increase in the frequencies of all skeletal parts. This implies better conditions for preserving bones of all kinds, regardless of size and density, and argues against accumulation due to selective processes of sorting (which would tend to concentrate bones of similar sizes or densities or both).

TABLE 7. THE SQUARE FREQUENCIES OF REPTILE AND MAMMAL SKELETAL PARTS IN THE SEVEN SAMPLE LOCALITIES. FREQUENCIES ARE CALCULATED AS THE NUMBER OF SQUARES WITH A PARTICULAR ELEMENT DIVIDED BY THE TOTAL NUMBER OF SQUARES IN EACH LOCALITY. THE FREQUENCIES OF ASSOCIATED PARTIAL SKELETONS AND JUVENILE BONES ARE CALCULATED IN THE SAME MANNER. MAMMAL AND REPTILE BONES ARE COMBINED IN THE SECOND LISTING TO INCLUDE THOSE WHICH COULD NOT BE DEFINITELY ASSIGNED TO ONE OR THE OTHER CLASS. THIS SHOWS THE RELATIVELY HIGH PROPORTION OF RIB AND DIAPHYSIS FRAGMENTS IN THE TOTAL BONE SAMPLE.

REPTILE	DELTA				CHANNEL		FLOOD-PLAIN
	130-0201	105-0208	103-0267	103-0256	102-0201	105-1311	8+6-0104
Tooth	.86	.85	.50	.33	.26	.68	.12
Skull/jaw	.10	.05	.30	.07	.15	.08	.00
Vertebra	.19	.05	.15	.19	.18	.00	.02
Limb	.14	.05	.05	.15	.09	.00	.00
Scute	.24	.40	.50	.30	.24	.40	.02
Phalanx	.10	.15	.00	.04	.00	.04	.00
Carapace/ plastron	.24	1.00	.70	.81	.24	.32	.12
# occurrences per square (average)	1.9	2.5	2.2	1.9	1.1	1.1	.3

MAMMAL AND REPTILE							
Tooth	.95	1.00	.80	.59	.76	1.00	.67
Rib	.76	.90	.85	.63	.53	.64	.32
Pelvis	.14	.25	.25	.04	.06	.16	.05
Diaphysis	.57	1.00	.95	.89	.71	.92	.55
Phalanx	.52	.55	.35	.30	.15	.32	.12
Vertebra	.57	.85	.55	.59	.29	.48	.15

RELATIVE ABUNDANCE OF SKELETAL PARTS

The frequency data in Table 7 can be analyzed: 1), in terms of the most common bones in each locality and 2), in terms of the correlations between localities caused by similar proportions of different mammalian bones. Teeth are the most common mammalian element in all localities except 103-0256. Otherwise, the patterns of frequency are variable, with some indication that vertebrae and phalanges concentrate in the deltaic environments. In order to clarify possible correlations between lo-

calities, two numerical analyses were used: a multiple regression analysis, which gives correlation coefficients for locality to locality comparisons, and a Q-Mode Factor Analysis, which shows groupings of the localities in terms of skeletal parts.

CORRELATIONS BASED ON BONE ABUNDANCE

Figure 20 shows a correlation matrix resulting from multiple regression treatment of skeletal part frequencies in the squares. The correlation is "Pearson's product moment correlation" which assumes con-

TABLE 7 (CONT.)

MAMMAL	DELTA				CHANNEL		FLOOD- PLAIN
	130- 0201	105- 0208	103- 0267	103- 0256	102- 0201	105- 1311	8+6- 0104
Tooth	.67	.85	.70	.56	.62	1.00	.52
Jaw part	.24	.10	.10	.04	.21	.08	.09
Maxilla	.05	.00	.00	.00	.00	.00	.02
Cranial part	.05	.25	.15	.07	.12	.08	.08
Horn core	.19	.25	.35	.15	.18	.36	.03
Vertebra	.48	.75	.50	.59	.15	.36	.15
Sacrum	.00	.00	.05	.04	.00	.00	.00
Scapula	.14	.45	.15	.15	.12	.20	.09
Pelvis	.10	.20	.20	.04	.03	.12	.05
Humerus	.19	.50	.30	.11	.06	.20	.14
Radius/ulna	.14	.40	.20	.11	.15	.20	.15
Femur	.14	.40	.05	.07	.18	.16	.08
Tibia	.10	.30	.25	.07	.06	.28	.14
Patella	.05	.05	.00	.00	.00	.04	.00
Metapodial	.10	.40	.40	.22	.18	.32	.14
Astragalus	.10	.20	.25	.11	.03	.08	.14
Calcaneum	.10	.15	.15	.15	.00	.12	.08
Podial	.10	.45	.10	.19	.24	.20	.18
Phalanx	.48	.65	.35	.26	.15	.28	.12
Total # squares	21	20	20	27	34	25	66
# occurrences per square (average)	3.4	6.4	4.2	2.9	2.4	4.1	2.2
Associated parts	.04	.20	.05	.04	.00	.00	.06
Juveniles	.14	.30	.05	.04	.06	.12	.00
% hippo bones	18%	16%	21%	6%	12%	7%	2%

Total # squares for all localities: 213

Average occurrences per square: $690/213 = 3.2$

tinuous data and normal bivariate distributions. Both conditions are satisfactorily met by the squares data. Correlations are based on the five most common elements: teeth, vertebrae, phalanges, scapulae and radii/ulnae.

An obvious feature of all the correlations is that they are high ($> .5$). This shows a basic similarity in the ratios of the five skeletal elements in all the sample assemblages, although these elements vary greatly in size and density. Therefore, the

differences in the sedimentary environments were not enough to alter the basic similarity of the thanatocoenoses sampled in each deposit. This similarity is probably produced by those bones most likely to survive carnivore activity and become sedimentary particles.

Many of the correlations shown in Figure 20 are significantly different, in spite of the overall similarity. The highest and lowest coefficients differ significantly, with a probability of $< .05$ according to the "z test"

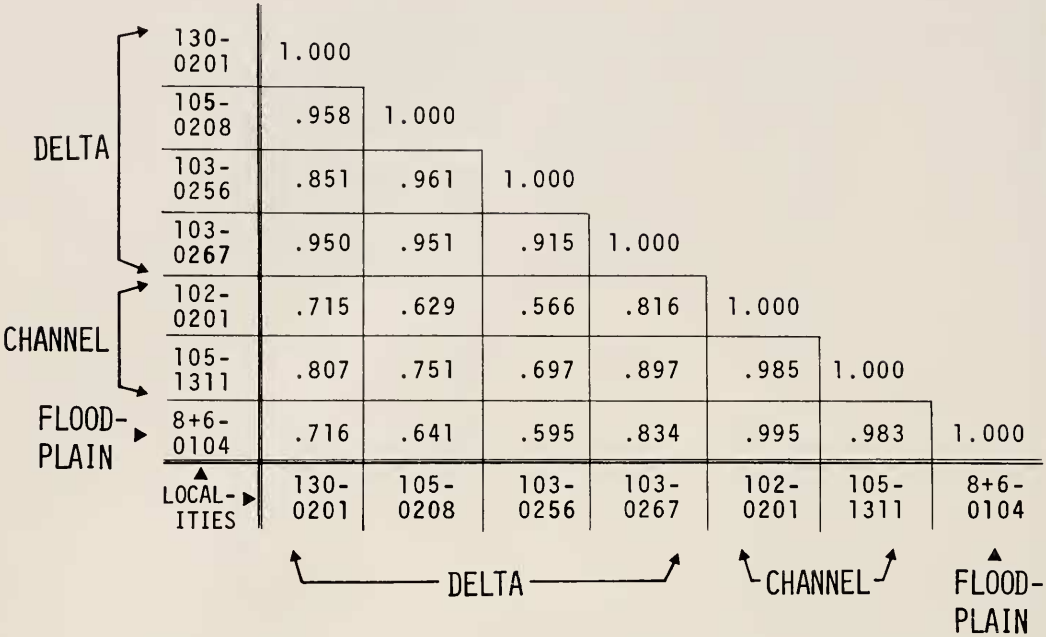


Figure 20. Correlation coefficients (Pearson's product moment correlation) between sampling localities according to the proportions of the five most common skeletal parts: teeth, vertebrae, phalanges, radii/ulnae and scapulae. Highest correlations show strong similarities between channel and floodplain environments in terms of the proportions of different skeletal parts.

for significance (Simpson *et al.*, 1960:246). Other coefficients are indicative of trends even when their differences are not within the acceptable limits of significance ($p \leq .05$).

The coefficients show that the channel assemblages, 105-1311 and 102-0201, are closely correlated with each other and with the floodplain, 8+6-0104. The deltaic assemblages have relatively low correlations with the floodplain, variable degrees of correlation with the channels, and high correlations among themselves. Thus the proportions of the five different bones are similar in similar sedimentary environments, showing the effects of processes operating within these environments. Some of the close interenvironmental correlations, such as between the floodplain and channel assemblages, and between 130-0201 and 103-0267, suggest processes that are common to more than one sedimentary situ-

ation. These can be further clarified by examining which bones are influential in causing the interlocality correlations.

FACTOR ANALYSIS OF THE
BONE ASSEMBLAGES

Factor analysis was used to indicate which skeletal parts cause similarities or differences among the seven bone assemblages. The Q-Mode Factor Analysis, "CABFAC," was run on the frequency data from all of the mammalian skeletal parts. A solution of three varimax factors (axes placed within the data array) explains 97% of the total variance in the assemblages. The projection of the data for each locality on these axes is plotted on the triangle diagram shown in Figure 21. The diagram shows graphically how the three factors group (cluster) the bone assemblages.

The three factors consist of 1) vertebrae

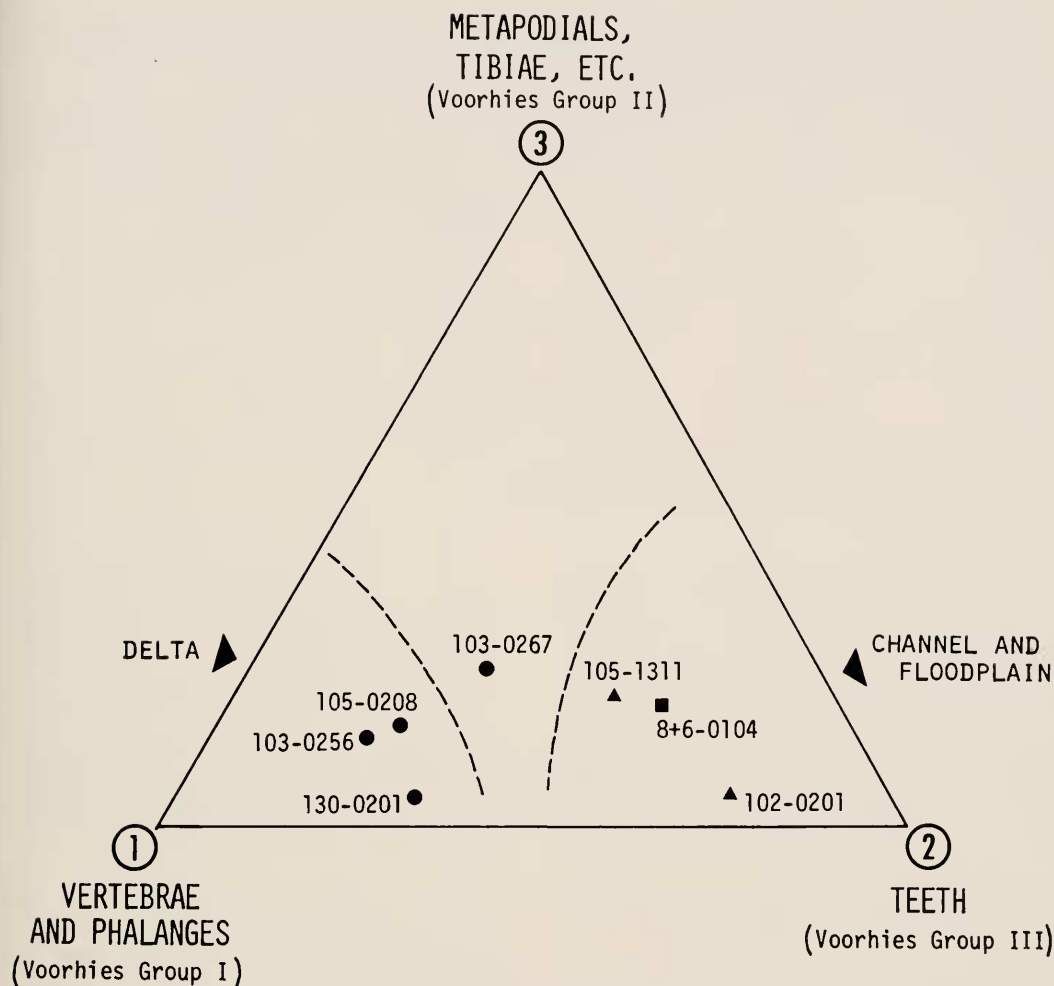


Figure 21. Triangle diagram showing the results of a three-factor analysis of the frequency data for all mammalian bones. The factors correlate with Voorhies' dispersal groups, showing a relatively high proportion of Group I (most easily dispersed) in the deltaic assemblages and Group III (lag) in the channel and floodplain assemblages.

and phalanges, 2) teeth, 3) limb parts such as tibiae, metapodials, and astragali. The triangle diagram shows a clear separation of assemblages on the basis of Factors 1 and 2. The three deltaic localities have a high proportion of vertebrae and phalanges, while the channels and the floodplain have high proportions of teeth. 103-0267 falls between the two groupings, and is somewhat anomalous in its lack of similarity to the channel assemblages. Localities 103-

0267 and 8+6-0104 both show that there is no strict correlation between tooth concentrations and coarse-grained sediment. 103-0267 is a coarse-grained deposit lacking a high proportion of teeth; 8+6-0104 is fine-grained, but is characterized by a high tooth concentration.

It is clear that the high correlation coefficients between assemblages from similar sedimentary environments are due to the proportions of teeth, vertebrae and

TABLE 8. THE RELATIVE FREQUENCIES OF SKELETAL PARTS IN A SINGLE SKELETON, THE AVERAGE OF BOVID, SUID, EQUID AND HIPPO SKELETAL PROPORTIONS. UNDERLINED PARTS ARE THOSE WHICH ARE MOST COMMON OR MOST CONSISTENTLY PRESENT IN THE FOSSIL ASSEMBLAGES.

	No. in average skeleton	No. of each part/total no. of parts in average skeleton (156)		No. in average skeleton	No. of each part/total no. of parts in average skeleton (156)
Teeth	38	.26	<u>Radii/Ulnae</u>	2	.01
Jaw	1	.01	Femora	2	.01
Maxilla	1	.01	Tibiae	2	.01
Cranium	1	.01	Patellae	2	.01
Horn Cores	2	.01	Metapodia	4	.03
<u>Vertebrae</u>	28	.18	Astragali	2	.01
Sacrum	1	.01	Calcanea	2	.01
<u>Scapulae</u>	2	.01	Podials	22	.14
Pelvis	1	.01	<u>Phalanges*</u>	42	.27
Humeri	2	.01			
			TOTAL	156	

* Including metapodials of suid and hippopotamus.

phalanges. These two groups of skeletal parts have very different properties of density and destructibility. The deltaic environments preserve more of the easily transported and destructible elements, the vertebrae and phalanges. The channel and floodplain environments preserve more of the denser and durable parts, primarily teeth. The experimental data on bone transport discussed in the section on bones as sedimentary particles can be used to interpret these differences in the fossil assemblages.

COMPARISONS WITH VOORHIES GROUPS

The Voorhies Groups consist of bones with very different dispersal potentials. For animals from suid- to equid-size, phalanges and vertebrae are included in Group I, limb parts in Group II to III and teeth in Group II-III. Group I is most easily transported, Group III least easily transported and Group II intermediate, in currents up to 150 cm/sec, given Voorhies' (1969) experimental conditions.

The three factors shown in Figure 21 are closely comparable to the three Voorhies Groups. Group I is more typical of the deltaic assemblages and Group II of the channel and floodplain assemblages. This

provides evidence that transport sorting may be an important process in creating differences between the bone assemblages, i.e., the lag group is left behind in the channels while the transportable group is carried out to the deltaic and lacustrine deposits. The loss of Group I in the floodplain may result from winnowing of the lighter elements during floods, if the current velocities on the floodplain exceed 10-20(?) cm/sec.

SINGLE SKELETON COMPARISONS

Comparisons of the bone frequency data with the percentages of different bones in a single, whole skeleton show how the assemblages have been altered from their original states. If all bones had been preserved together, then the correlations between the proportions of different parts in the sample assemblages and a single skeleton should be high.

Average proportions of parts in a single skeleton were calculated, combining the most common mammal groups in the fossil assemblages. These consist of bovids, hippos, suids and equids. Frequencies of the different parts are given in Table 8. Figure 22 shows the comparison of fossil and single skeleton bone frequencies for

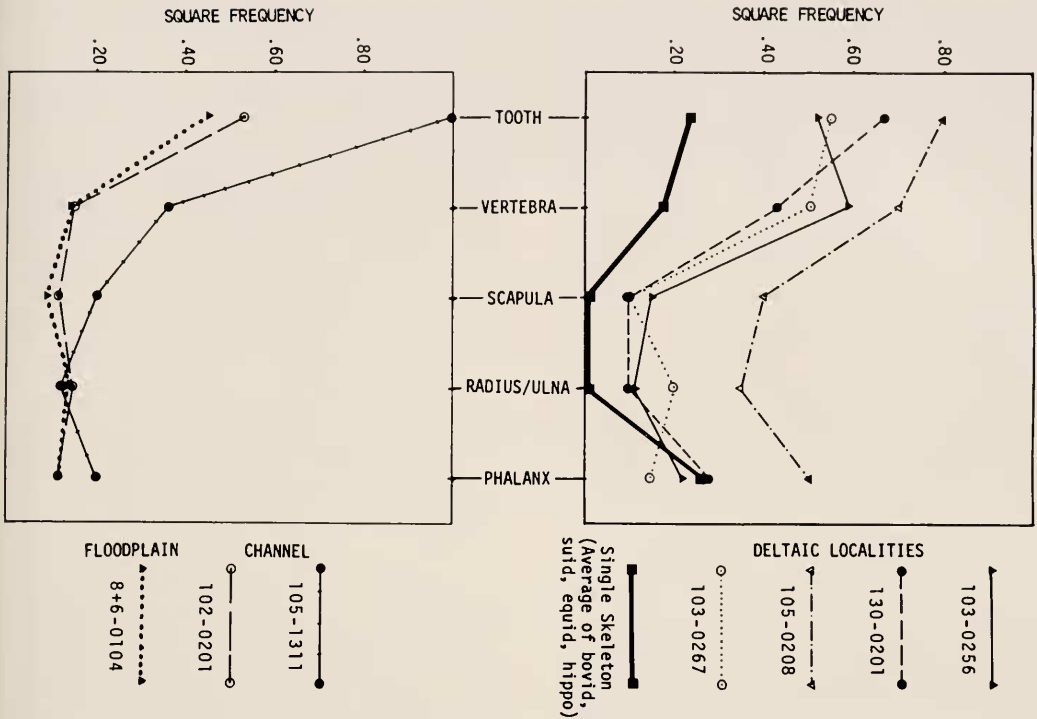


Figure 22. The square frequencies of the five most common mammalian skeletal elements in each locality compared with the proportions of the same elements in a single, average skeleton. The localities separated by factor analysis (Fig. 21) are distinct in their degree of alteration from single skeleton proportions.

the 5 most common or most consistently occurring parts. The assemblages fall into two obvious groups: 103-0256, 130-0201, 105-0208 and 103-0267 are closely correlated with the single skeleton, and 105-1311, 102-0201 and 8+6-0104 are not.

It appears that the lacustrine-deltaic environments, plus the 103-0267 channel-beach complex, preserve skeletal parts with a minimum of change from the original proportions. This implies the absence of processes that would sort the bones according to size, density or destructibility. In contrast, the channels, 102-0201 and 105-1311, and the floodplain, 8+6-0104, preserve altered assemblages with a high proportion of the heavier and more durable parts and a much lower proportion of the lighter and more destructible elements.

DISCUSSION OF EVIDENCE FOR TRANSPORT SORTING

The combination of evidence from the comparisons of bone assemblages with Voorhies Groups and single skeletons leads to important conclusions regarding the histories of the bones in each locality. In the deltaic deposits, bones from all Voorhies Groups are present in proportions similar to those of an average single skeleton. Therefore, the major component of Group I in these deposits is probably not transported from elsewhere (i.e., the channels). If it were, then it has combined with lag assemblages to closely approximate the proportions in one skeleton. A better interpretation for the deltaic assemblages is that they have not been sorted. The relatively

fresh, unabraded surface textures of many of the bones, plus their lack of hydraulic equivalence with matrix grain sizes, further supports this interpretation. The high proportion of Voorhies Group I in the deltaic assemblages is a product of nonselective taphonomic processes rather than selective ones.

In the 105-1311 and 102-0201 channels, the concentration of teeth is the result of sorting by fluvial processes. This sorting combines the lag concentration of teeth because of their greater density *and* because of their greater durability in transport situations. In addition, teeth are probably concentrated from floodplain deposits as the channel migrates laterally, eroding its banks. Other parts derived from re-excavated skeletons would not be likely to survive erosion unless already mineralized.

The 103-0267 distributary-beach complex combines the sedimentary characteristics of the other channels with a bone assemblage similar to the deltaic ones. The assemblage shows lack of selective sorting, and apparently a large lag component of teeth was not a product of the fluvial processes operating in 103-0267. Why this should be so is as yet unexplained.

The floodplain assemblage shows selective preservation of teeth in a fine-grained sedimentary context. As mentioned on p. 536, this indicates the removal of lighter elements from an untransported thanatocoenose. Such removal could result from winnowing out of the light parts or from surface weathering and preferential destruction of vertebrae and phalanges relative to teeth. The relative importance of these two processes can be determined by future experimental work on the critical entrainment velocities of vertebrae and phalanges, and by observation of thanatocoenoses on modern floodplains. The low frequency of horn cores in 8+6-0104 may provide a clue indicating selective destruction by weathering, since in modern situations horn cores are often destroyed by worms that feed on their organic constit-

uents (H. B. S. Cooke, personal communication) (Plate 3).

The extent to which sedimentary processes have altered the bone assemblages is clear from the examination of bone frequencies. The deltaic assemblages are least altered, and probably represent autochthonous accumulations in sedimentary environments where the potential for rapid burial, without re-excavation, is high. The floodplain assemblage is also autochthonous but has been altered by taphonomical processes so that it resembles the channel assemblages. These show the most extensive alteration of bone ratios due to sedimentary processes. 103-0267 is intermediate in the degree to which taphonomic processes have affected the bone assemblage.

The most useful localities for paleo-ecologic information are thus established as the deltaic and floodplain environments. The channels will also prove useful, since the factors contributing to their bone assemblages are known. They will include a mixture of animals from the vicinity of a fluvial system, in contrast to deltaic deposits, which preserve animals that frequented lake margin habitats.

ADDITIONAL ASPECTS OF THE BONE ASSEMBLAGES

More information regarding taphonomic history can be drawn from bone characteristics unrelated to relative abundance. These include the occurrences of associated skeletal parts and the ratios of proximal and distal ends of limb bones.

Associated parts of skeletons are rare in the East Rudolf deposits in general. The frequencies of these in the sample localities are included in Table 7. The channels 105-1311 and 102-0201 have none, while the floodplain and deltaic localities, including 103-0267, have at least one. Most of these consist of associated vertebrae, with more complete partial skeletons occurring in 105-0208 and 8+6-0104.

The associated skeletal parts may result

TABLE 9. TOTALS OF PROXIMAL (P) AND DISTAL (D) LIMB ENDS IN THE FOSSIL ASSEMBLAGES FROM EACH SAMPLE LOCALITY.

		DELTA				CHANNEL		FLOOD- PLAIN	TOTAL
		130- 0201	105- 0208	103- 0267	103- 0256	102- 0201	105- 1311	8+6- 0104	
Humerus	P	2	2	2	0	3	2	2	13
	D	3	8	1	3	2	2	7	26
Radius/ ulna	P	1	11	3	1	2	1	10	29
	D	1	1	2	1	1	1	4	11
Femur	P	1	4	1	0	2	1	3	12
	D	4	5	1	2	5	3	2	22
Tibia	P	1	4	1	1	1	5	5	18
	D	2	1	2	3	4	3	6	21
Metapodial	P	4	1	4	5	0	3	6	23
	D	1	6	6	2	1	2	8	26
Total	P	9	22	11	7	8	12	26	95
	D	11	21	12	11	13	11	27	106

from carcasses buried at the site of death or from carcasses transported by flotation. There are very few criteria that could be used to distinguish between these two possible taphonomic histories. However, the associated parts do indicate a minimum of reworking of the bone assemblages after initial burial. This agrees well with other evidence for lack of reworking of the delta margin and floodplain assemblages. The absence of associated parts in the channels is consistent with the abraded surface textures of the bones as an indication for extensive reworking of sedimentary particles in the channel environments.

Most of the limb bones in the samples are represented by one end or the other. It is of interest to determine whether some ends are more common than others, as an indication of preferential sorting or destruction prior to burial.

The numbers of proximal and distal ends of the major limb bones are listed in Table 9. For all localities and all limbs combined, the totals of 95 proximal and 106 distal are very close to a 1:1 ratio. This might be interpreted as indicating that no more proximal than distal ends are preserved, or

vice versa. When the totals for each limb in all localities are examined, however, the relative frequencies of proximal and distal ends prove to be quite variable. There are nearly twice as many distal as proximal ends of humeri and femora, and many more proximal ends of radii/ulnae than distal. From the density measures of proximal and distal recent bones given in Appendix 2, it is apparent that the denser end is more commonly preserved in humeri and radii/ulnae, while the lighter end is more common in femora. A model for differential preservation because of transport sorting or more rapid weathering of low density ends does not fit this evidence.

The differences in frequency of the proximal and distal ends can best be explained by carnivore activity. In animals killed by carnivores or scavenged after death, the limbs are usually pulled off the carcass at the proximal articulation (humerus/scapula and femur/pelvis joints) (Müller, 1957:256-258). Proximal ends of the humerus and femur would be subjected to stress and later exposed for gnawing. In contrast, the elbow and knee joints are more likely to remain held together by

ligaments and survive the bone-crushing activity directed at more nourishing parts such as marrow-filled diaphyses. This explains the relatively high proportion of distal humeri and femora. The disproportionate number of proximal "radii/ulnae" actually consist primarily of olecranon processes from the ulnae. These are ligament-covered, lack a marrow cavity, and thus would survive better than the distal ends of radii.

The pattern of proximal and distal limb element frequencies can be regarded as good evidence for carnivore activity in fossil assemblages in general. Such evidence has also been used by Voorhies (1969:20) to indicate carnivore activity prior to the final burial of the Pliocene Verdigre Quarry bone assemblage. For the East Rudolf localities, the evidence for carnivore activity can be detected in spite of differences in the taphonomic histories of the bone assemblages in the different depositional environments.

THE REPTILIAN ASSEMBLAGES

Reptilian parts form less consistent frequency patterns than those of mammals. The most common elements, as shown in Table 7 are crocodilian teeth and chelonian shell parts. The relative numbers of crocodilian parts are very similar from locality to locality. There is no indication of any increase in similarity between assemblages from similar sedimentary environments. This is probably a result of the universal availability of crocodile bones in the aquatic (generally depositional) environments where crocodiles live. The low frequency of crocodiles in the floodplain environment, which crocodiles do not usually frequent, emphasizes this point. The chelonian shell parts are variable in occurrence, and are slightly more abundant in the deltaic deposits including 103-0267. This suggests some correlation between the more aquatic sedimentary environments and the chelonian occurrences.

Conclusions Concerning the Bone Assemblages

The evidence given in the preceding two major sections of this study brings out a number of taphonomically important factors that can be combined to support a definite history for any given vertebrate fossil assemblage comparable to those occurring in the Koobi Fora Fm.:

- 1) The correlation of bone assemblages with dispersal groups from Voorhies' flume study
- 2) The correlation of bone assemblages with the proportions of a single skeleton
- 3) The comparison of hydraulic equivalents of bones with grain sizes in the associated sediments
- 4) The completeness of bones, and surface characteristics that indicate presence or absence of weathering or abrasion prior to burial
- 5) Presence or absence of articulated or associated skeletal parts
- 6) Ratios of proximal and distal ends of limb bones that deviate from 1:1

All of these factors provide a basis for interpreting the East Rudolf data. The bone frequencies for each locality thus can be used to determine the taphonomic histories of the vertebrate assemblages. The following points can be made:

- 1) The different sedimentary environments of East Rudolf show a general similarity in the compositions of their mammalian bone assemblages. The same bones are present in all environments, and none of the assemblages consist exclusively of one of the three Voorhies Dispersal Groups.
- 2) Evidence for a certain degree of sorting and redistribution of bones is present in the different sedimentary environments. Significant differences in relative numbers of different bones are shown by the concentrations of teeth in the channels (105-1311 and

102-0201) plus the floodplain (8+6-0104), and by the concentrations of vertebrae and phalanges in the deltaic localities (130-0201, 105-0208, 103-0256, 103-0267). These can be correlated with the sorting effects of taphonomic processes in the channels and on the floodplain, and the absence of sorting on the delta/margins.

- 3) Consideration of the bone frequencies in the light of Voorhies Groups, hydraulic equivalence and single-skeleton comparisons shows that autochthonous and allochthonous assemblages of fragmental vertebrate bones can be distinguished. The deltaic and floodplain localities consist of basically autochthonous vertebrate fossils, while the channels contain a mixture of allochthonous and autochthonous assemblages.

FAUNAL ASSEMBLAGES OF THE KOOBI FORA FORMATION

Taphonomic analysis has shown that all of the sample fossil assemblages can be considered autochthonous in the broadly defined deltaic and fluvial environments. It is now possible to examine the faunal compositions of the seven bone assemblages and to relate these to the different sedimentary environments. Comparisons can be made from environment to environment which should indicate true paleoecologic differences or similarities in the faunas. In the following discussion, several aspects of the paleoecology of the Kooibi Fora Fm. and its vertebrates will be given particular attention. These include the differences in numbers of aquatic and nonaquatic vertebrates, the relative frequency of different terrestrial mammals in the different environments, and the patterns of occurrence of mammalian groups that have close counterparts in modern ecosystems.

The fauna from the square sample as a whole includes 14 out of the 20 major vertebrate groups listed by Maglio (1972: 380-381) for the Kooibi Fora Fm. The

sample assemblages also include most of the genera of bovids, suids, equids and hippos. The carnivores listed by Maglio (1972:380-381) are the most poorly represented groups in the samples used for this study.

Method of Identification

The fossil collections consist of material that can be identified at a number of different taxonomic levels. Major groupings of vertebrates used for faunal comparisons among the sample localities were designated so that each member of a group has approximately equal numbers of identifiable parts. In practice, for example, this amounted to teeth, skull parts, limb ends and foot parts for mammals. The mammals listed below could be identified equally well using any of these parts. Consideration of this factor was necessary to prevent undue biasing of the square frequency for a form with substantially more or less identifiable parts. The fossil assemblages can be divided into faunal groups, corresponding roughly to several taxonomic Categories, as follows:

1) Class: Mammal, Reptile, Bird, Fish. Identifications were based primarily on the morphology of the bone fragments. Bone micro-structure was useful as a distinguishing character for very small fragments. In some cases parts of pelves, scapulae, ribs and diaphyses could not be certainly assigned either to mammal or reptile, and such parts are not included in any of the totals.

2) Groups of Reptiles and Mammals.

<i>Mammals</i>		<i>Reptiles</i>
Elephant	Suid	<i>Crocodylus</i>
Deinother	Equid	<i>Euthecodon</i>
Hippopotamus	Primate	Trionychid
Rhinoceros	Carnivore	Pelomedusid
Giraffe	Rodent	<i>Geochelone</i>
Bovid		Varanid

The common denominator in these groups is that they are approximately equally identifiable, within each list. For

example, using the figures for relative numbers it will be possible to determine whether there are more hippos than elephants in the sample assemblages, but not whether there are more hippos than trionychids. Some of the reptiles produce many more abundant and readily identifiable bones than do the mammals (e.g., crocodile scutes), and may appear relatively more abundant in the samples. Thus, relative frequencies are only comparable *within* the mammals and reptiles, and some caution should be observed in comparing the different reptilian groups as well. *Crocodylus* and *Euthecodon* are comparable since they were identified only on the basis of teeth, and the three chelonian groups should be comparable since only shell parts were used. Problems in separating small *Geochelone* from Pelomedusids may lower the abundances of these two groups relative to the Trionychids.

3) Groups of Suids, Equids, Bovids and Hippos.

Suids	Equids
<i>Mesochœrus</i>	<i>Equus</i>
<i>Notochoerus</i>	<i>Hipparion</i>
<i>Metridiochoerus</i>	(= "Stylohipparion")
Bovids*	Hippos
Alcelaphinae	<i>Hippopotamus</i> sp. (large)
Large	<i>H.</i> sp. nov. (small)
= <i>Megalotragus</i>	(S. C. Savage,
Small	personal communication)
= <i>Damaliscus</i> -like	
Reduncinae	
Tragelaphini	
Bovini (<i>Pelovis</i>)	*Nomenclature after Ansell (1971).

These groups occur in significant abundance in the sample assemblages and can be compared between localities. Other groups are represented by only one or two occurrences and cannot be used for comparative purposes. These include the bovid groups Antilopini, Hippotraginae, Cephalophinae and Neotragi, and a suid that is probably *Potomachoerus*.

Identification of the suids was done only on the basis of teeth. The equids were distinguished using teeth and metapodials, and the hippos using relative size of the skeletal parts identifiable as hippo. Bovids were identified primarily on the basis of teeth, but also from horn cores, ends of limb bones, podials and phalanges. The bone samples were equally identifiable within each of these groups. However, when the groups are compared, the suid and equid genera will have lower apparent abundances than the bovid tribes and subfamilies since they are represented by many fewer identifiable parts.

Although various other groups of vertebrates are identifiable to genera and species, they are not discussed in this study. These include primarily the fish and chelonians. Future work may reveal interesting patterns of abundance for members of these groups in the different sedimentary environments.

The relative numbers of all vertebrate groups will be expressed as "square frequencies," the percentage of squares in a locality that contain a given animal. This is the same measure as that used for skeletal parts (p. 529), and represents the "dispersed" or overall abundance of an animal in a sample locality.

Abundance of Vertebrate Classes

The class frequencies (Table 10) show that mammals, reptiles and fish are well represented in all seven localities. Birds occur in low frequency in two deltaic localities and in the floodplain. Mammals are at least as abundant as reptiles and fish in nearly all localities. Since most of the mammals are terrestrial, while the fish and most of the reptiles are aquatic, the relative numbers of vertebrate classes in the channels and deltas is not directly related to which animals were actually living within the depositional environments. Otherwise, fish and reptiles should be more common

TABLE 10. CLASS ABUNDANCE IN TERMS OF SQUARE FREQUENCY.

	Delta				Channel		Floodplain
	130-0201	105-0208	103-0267	103-0256	102-0201	105-1311	8+6-0104
Mammal	.90	1.00	1.00	1.00	.82	.82	.83
Reptile	.90	1.00	.95	.89	.62	.62	.18
Bird	.00	.15	.00	.07	.00	.00	.03
Fish	1.00	1.00	.95	1.00	.79	.79	.30

than mammals. The large proportion of mammalian fossils probably means that there was a greater large vertebrate biomass in the terrestrial habitats close to the depositional environments. In the floodplain (8+6-0104), the relative numbers of the classes are more closely correlated with nonaquatic habitat preferences, and fish and reptiles are much less abundant than the predominantly terrestrial mammals.

Overall, the deltaic environments have a larger proportion of fish and reptiles than the channels. This is consistent with the more permanent and extensive lacustrine-deltaic aquatic environments, particularly if the nondeltaic channels were seasonally dry.

Calculated correlation coefficients based on the class frequencies are high among all localities (.97-.99) except for 8+6-0104. Here, the larger number of terrestrial animals over aquatic reflects a basic paleoecologic distinction consistent with the geologic interpretation of the floodplain environment for 8+6-0104. In this case, and probably for many similar fossil-bearing environments throughout the geologic record, the fauna which is preserved is primarily terrestrial. The deltaic and channel environments, in contrast, consistently preserve mixtures of aquatic and nonaquatic animals.

Abundance of Vertebrate Groups

Much paleoecologic information is available from the relative frequencies of the groups of mammals and reptiles listed on p. 541. The East Rudolf samples are best suited for such analysis since they

provide abundant, easily identified fossil material representing these groups. The relative frequencies of mammals and reptiles are given in Table 11 and discussed below.

REPTILES

Three groups of reptiles are represented: crocodilians, chelonians and squamata. The last is rare, and the sample consists of a few vertebrae comparable in size to those of *Varanus* (Monitor Lizard). Crocodilians and chelonians occur in all areas, with chelonians more variable in relative abundance.

The crocodilians can be separated into two groups (Genera): *Crocodylus* (represented by at least two species) and the long-snouted *Euthecodon* (represented by at least one species). The two groups occur in similar frequencies except in 130-0201 and 102-0201, where *Crocodylus* is more abundant, and 103-0256, where *Euthecodon* is more common. It is unlikely that sorting during transport had any significant effect on the frequencies, since the hydraulic properties of the teeth are similar. Therefore, it is valid to conclude that, in general, the two crocodilians occupied overlapping ranges, i.e., both were present in the deltaic and channel environments. The living, long-snouted relatives of *Euthecodon* (*Tomistoma*) are found in quiet, open water (A. Greer, personal communication). Specific habitat preferences of *Euthecodon* are not clear from its patterns of abundance in the sample localities at East Rudolf. However, the conditions in 103-0256 after the transgression of the lake seem to have

TABLE 11. THE SQUARE FREQUENCIES OF THE MAMMAL AND REPTILE FAMILIES, CALCULATED AS THE NUMBER OF SQUARES WITH IDENTIFIABLE PARTS OF EACH FAMILY DIVIDED BY THE TOTAL NUMBER OF SQUARES FOR EACH AREA.

MAMMALS	DELTA				CHANNEL		FLOOD- PLAIN
	130- 0201	105- 0208	103- 0267	103- 0256	102- 0201	105- 1311	8+6- 0104
Elephant	.05	.25	.10	.04	.09	.36	.05
Dinothere	.00	.00	.00	.00	.12	.08	.00
Hippopotamus	.62	.85	.70	.37	.41	.92	.21
Rhinoceros	.00	.00	.10	.00	.06	.12	.02
Giraffe	.00	.15	.05	.00	.03	.28	.06
Bovid	.62	.75	.70	.63	.50	.96	.58
Suid	.29	.60	.20	.19	.32	.60	.27
Equid	.14	.30	.15	.11	.12	.56	.12
Primate	.05	.20	.00	.04	.06	.12	.03
Carnivore	.00	.05	.00	.00	.00	.04	.03
Rodent	.05	.00	.00	.00	.00	.04	.00
REPTILES							
<u>Crocodylus</u>	.86	.60	.45	.04	.21	.52	.09
<u>Euthecodon</u>	.48	.65	.55	.33	.12	.52	.03
Trionychid	.19	.70	.45	.30	.18	.25	.03
Pelomedusid	.05	.75	.20	.48	.00	.60	.08
<u>Geochelone</u>	.00	.05	.25	.33	.03	.04	.00
Varanid	.00	.05	.00	.04	.00	.04	.02

been exceptionally favorable to *Euthecodon* and not so to *Crocodylus*. Many articulated parts, including complete skulls, have been found in 103-0256 in addition to the samples from the squares.

The chelonian sample consists of three family groups: Trionychids, (soft-shelled aquatic turtles), Pelomedusids, (semi-aquatic to aquatic turtles), and *Geochelone*, (land tortoise) (Loveridge, 1941; Loveridge and Williams, 1957). Both aquatic forms are common in all localities except 130-0201, 102-0201 and 8+6-0104. Trionychids are most consistently abundant. The occurrences of *Geochelone* and the Pelomedusids do not conform to any consistent pattern that can be related to habitat preferences of their recent counterparts. The shell fragments have fairly low hy-

draulic equivalents (< 3 mm except for large *Geochelone*) and are readily transportable. This may affect the proportions of large and small turtles preserved in an assemblage, and would tend to concentrate large *Geochelone* in lag deposits. Sorting should not affect the relative frequencies of the other forms, if they are of comparable size ranges.

The pattern of chelonian occurrences in the fossil samples is not readily explained either by sorting or by inferred habitat preferences. Other factors are involved, and one of these probably concerns ecological preferences of the fossil turtles that cannot be adequately inferred from the modern ones without identification of the fossil material to species. This is further complicated by the probability that factors

influencing turtle abundance (e.g., water turbidity, vegetation) may not be evident from the sedimentary record.

The low frequencies of chelonians in the floodplain assemblage are consistent with all other evidence for its predominantly nonaquatic environment of deposition. In other localities, at least some crocodilians and chelonians inhabited the environments of deposition. This is indicated by the variety of skeletal parts of crocodilians present in all deltaic and channel assemblages (parts with a wide range of hydraulic equivalents). It is also indicated by the presence of associated, unreworke parts of both crocodilians and chelonians in many of the localities.

MAMMALS

The numbers of different mammalian groups represented varies among the localities (Table 11). The 105–1311 channel assemblage is most diverse, with 11 groups represented. 105–0208, which has the largest number of identifiable bones (2389), has a relatively low faunal diversity (8 groups). In general, the deltaic environments have lower numbers of different terrestrial mammals. The short time span postulated for the deposition of 103–0256 (the transgressive sand) may help to account for its low faunal diversity. As would be expected, the more terrestrial depositional environments preserve more kinds of terrestrial animals. As many mammal bones are preserved in the more aquatic environments as in the nonaquatic ones, but they represent fewer terrestrial groups. The relative diversity of the fossil mammal assemblages apparently gives a true representation of the greater diversity of forms in the more terrestrial habitats.

The most common groups in all localities are bovids, hippos, suids and equids. Bovid are the dominant forms in all assemblages except 130–0201, 105–0208, and 103–0267, where hippos are slightly more numerous. The frequencies given in graphic form in Figure 23, show similar patterns for most

of the assemblages. For the autochthonous assemblages of the deltaic and floodplain environments, these probably reflect the actual frequencies of animals in the death assemblages over the time periods sampled. The channel assemblages also should be broadly representative of the original relative abundance of the mammalian groups in the habitats sampled by fluvial processes. However, there is a definite bias against the smaller animals due primarily to their greater destructibility and transportability in all environments.

Rodents are rare throughout the East Rudolf vertebrate-bearing deposits. Since they are abundant in recent terrestrial habitats in the area, there can be little doubt that they are under-represented because of taphonomic processes that did not lead to preservation with the larger vertebrates. These probably involve carnivore destruction, rapid surface weathering of bones (due to high surface area to volume ratios) and high dispersal potentials (Dodson, 1974). The difficulties in collecting very small bones from the sample squares is another potentially important factor, although care was taken to minimize this during the sample collection.

Carnivores and primates have low frequencies in the samples, and this is partly a result of the same size factors affecting the rodent sample. However, some of the primates and carnivores reach sizes comparable to those of the smaller bovids and suids, and factors relating to size do not entirely explain the low frequencies. For carnivores, a low abundance compared with herbivores is consistent with their low relative biomass in the Eltonian Pyramid, in which a few carnivores are ecologically balanced with large numbers of herbivores. The scarcity of carnivore fossils probably reflects this ecological character. Primates are comparable in abundance to giraffes and rhinos in most localities. The samples consist primarily of baboons (*Simopithecus*), plus two occurrences of hominids (cf. *Australopithecus*, in the 105–1311 channel).

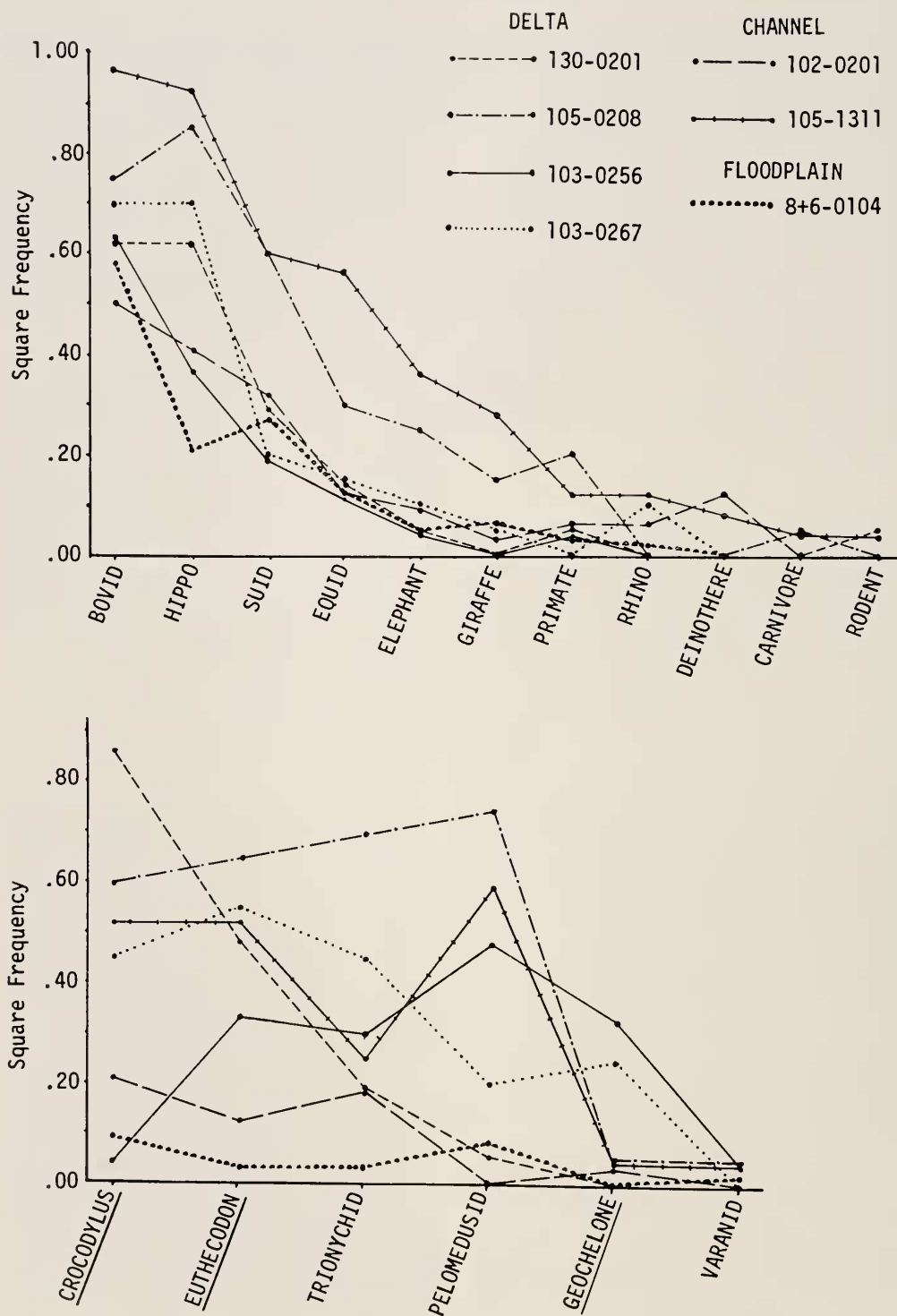


Figure 23. Comparisons of the square frequencies of mammal and reptile groups in the seven sample localities.

The relatively low frequency of primates is probably due to a combination of destructibility, high dispersal potential and lower original abundance or more localized groups than the better represented ungulate families.

The extinct *Deinotheres* are represented only in the 105-1311 and 102-0201 channels, together with rhinos. Rhinos also occur in the floodplain assemblage, in the *Loxodonta* Faunal Zone (Fig. 14), which may represent a time (~ 1.3 my.?) when *deinotheres* had become locally extinct. Neither is found in the deltaic environments sampled. Elephants, whose parts have similar low dispersal potentials, are found in all localities. The patterns of occurrence are best explained by habitat preferences, with the *deinotheres* and rhinos preferring dry, upland savanna and bush habitats while the elephants were more ubiquitous.

DISCUSSION OF THE MOST ABUNDANT MAMMALIAN GROUPS

The relative frequencies of the four most common groups, hippos, bovids, suids and equids, can be combined with data on the skeletal representation of each family for more detailed analysis of taphonomic and paleoecologic factors.

Comparisons of the frequencies given in Table 11 show that there is a close similarity between localities in the proportions of the four families, except in the cases of 103-0256 and 8+6-0104. The mammals of these localities include high frequencies of bovids and low frequencies of hippos. For the floodplain environment, this correlates nicely with the low representation of other aquatic forms. However, for the transgressive deposit in 103-0256, with its abundant aquatic fauna, the low proportion of hippos is anomalous.

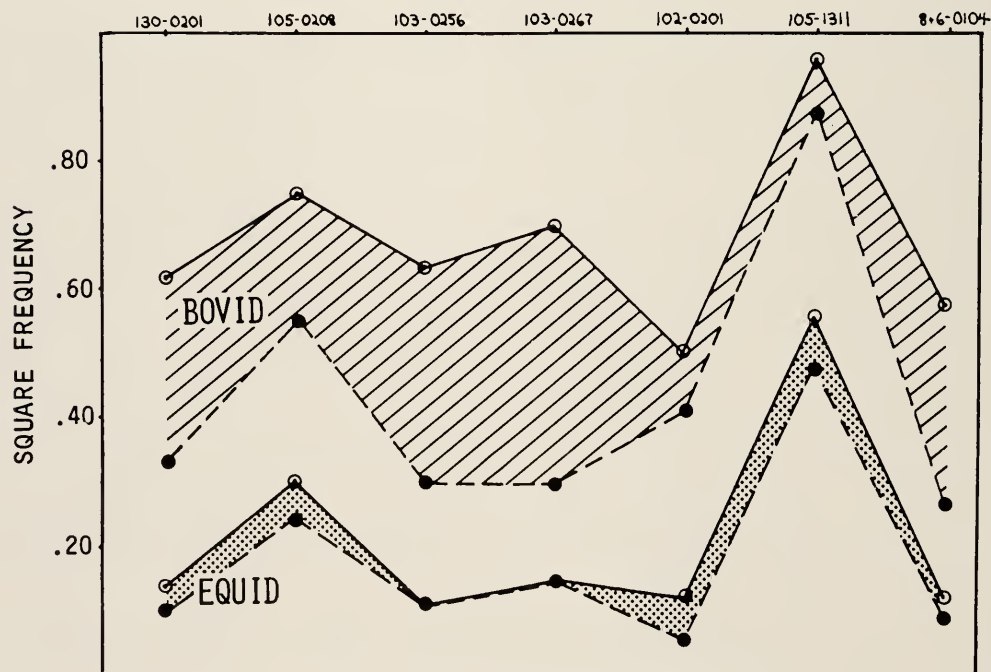
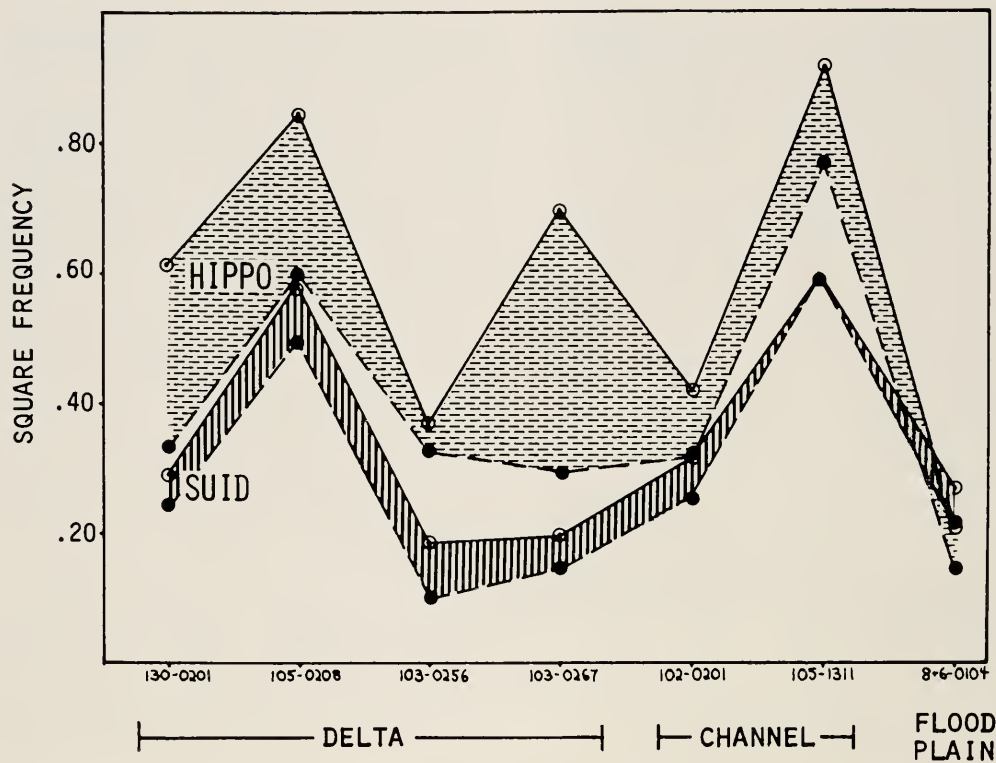
All four common groups are represented by teeth and other skeletal elements of different sizes and densities. These would

have different dispersal potential, according to the Voorhies Groups (Table 2) and size-density considerations. If any of the mammal groups were transported into the fossil assemblages as disarticulated skeletal parts, then they should be represented by a higher proportion of phalanges, podials, etc. Autochthonous animals should have mixed representation with teeth, limb parts, phalanges, etc.

For bovids and hippos, elements of widely variable original size and density occur together in all localities. These include teeth, phalanges and ends of limb bones, which fall into all three of Voorhies' dispersal groups. It is evident that these assemblages do not reflect extensive sorting by taphonomic processes. These processes may have been operating, particularly in the channels, but the bone input was enough to maintain an unsorted character in the assemblages. The best explanation for the skeletal representation is that the bone input was generally local, and the bovids and hippos are autochthonous with respect to the deltaic and fluvial environments.

Suids and equids are less abundant as fossils and are also represented by a lower diversity of skeletal parts. Both teeth and phalanges are present in the suid samples from all areas except 105-1311. Equids are represented by teeth, with only a few examples of other parts. The suid samples are more likely to be autochthonous since they combine elements of widely differing transport potential. The equid sample consists mainly of lag elements, many of which show evidence of transport abrasion. These are probably allochthonous in the channels, but are at least partly autochthonous in the floodplain and deltaic assemblages. For both suids and equids, the relatively low frequencies and poor skeletal representation imply lower original abundance than bovids in the floodplain and deltaic habitats.

The comparison of tooth frequency with the frequencies of all other elements is a



useful measure of the effects of taphonomic processes (weathering and transport) on the fossil assemblages. Figure 24 shows the frequencies of the four families in terms of all identifiable elements and in terms of teeth only. Where the lines diverge, a large proportion of the sample consists of parts other than teeth. Representation of hippos and bovids is similar in all localities except 103-0256 and 8+6-0104. The low frequency of hippos in these two assemblages is due to a lack of elements other than teeth. Since the bones from both localities are basically autochthonous, this emphasizes that there must have been relatively few hippos leaving bones in the original environments. The plots for suids and equids demonstrate the relatively greater numbers of teeth in these samples. The autochthonous or allochthonous context of these animals in the bone assemblages cannot be inferred from their skeletal representation, but is indicated by their *association* with autochthonous or allochthonous assemblages, as determined by the taphonomic histories of each assemblage as a whole.

The assemblage of 103-0267, which combines characteristics of channel and deltaic environments, includes a high proportion of different hippo and bovid skeletal parts, in contrast to the other channel assemblages. This indicates a closer similarity to the taphonomic histories of assemblages in 130-0201 and 105-0208, than to those of the other localities. Considering all evidence for 103-0267, it appears to have been much more permanently aquatic than the other channels. This would fit an interpretation of distributary channels close to the lake in association with beach environments.

It is of interest that the known aquatic or nonaquatic habits of bovids and hippos

cannot be inferred from their overall frequencies or skeletal representation in the deltaic or channel assemblages. Without knowledge of recent ecology, it would only be valid to say that both hippos and bovids are autochthonous in the deltaic and fluvial environments. Beyond this, anatomical studies would be necessary for interpreting ecological differences. The lesson in this is important for fossil assemblages with no modern counterparts: hippos and bovids are an example of two distinct groups with comparable fossil representation that *does not* necessarily reflect their ecological differences, even though one is more closely tied to aquatic habitats than the other.

Abundances of Selected Mammalian Groups

SUIDS

Three genera of suids are common in the fossil assemblages and occur in variable frequencies from locality to locality. Table 12 gives the frequency data for these genera, based only on teeth. *Notochoerus* and *Metridiochoerus* are combined since molar fragments of the two are difficult to distinguish. They are similar in having high-crowned, elongate third molars adapted to eating the relatively abrasive grasses, and both are thought to belong to the same group as *Phacochoerus*, the modern warthog (Cooke and Maglio, 1972: 312), which is generally an open-habitat form (Dorst and Dandelot, 1970:174). *Mesochoerus* is easily distinguished from the other suids by its low-crowned third molar. Its dentition is adapted to softer vegetation than in *Metridiochoerus* and *Notochoerus*. *Mesochoerus* is believed to be close to the ancestral stock of the recent

←

Figure 24. Comparisons of skeletal representation of the four most common mammal groups in each sample locality. Solid circles and dashed (lower) lines indicate the frequencies of all squares with teeth. Open circles and solid (upper) lines indicate the total square frequency, counting all teeth and bones. The space between the lines is large if a group is represented by parts other than teeth. Bovids and hippos show comparable skeletal representation except for the delta flats (103-0256) and the floodplain (8+6-0104).

TABLE 12. SQUARE FREQUENCIES OF SUID GENERA.

	Delta				Channel		Floodplain
	130-0201	105-0208	103-0267	103-0256	102-0201	105-1311	8+6-01014
<i>Notochoerus</i> / <i>Metridiochoerus</i>	.00	.20	.05	.04	.24	.24	.01
<i>Mesochœrus</i>	.14	.30	.00	.04	.03	.04	.08

Hylochoerus (Giant Forest Hog), a dense bush or forest animal (Cooke and Maglio, 1972:311).

Figure 25 shows that the *Notochoerus* group (= *Notochoerus* + *Metridiochoerus*) is far more common in the channel assem-

blages, and *Mesochœrus* is more typical of the deltaic assemblages. Chi-square tests (Simpson *et al.*, 1960) show that this difference is significant with $p \leq .05$. Paleoecologic separation of the two groups is strongly indicated, and in a way that is con-

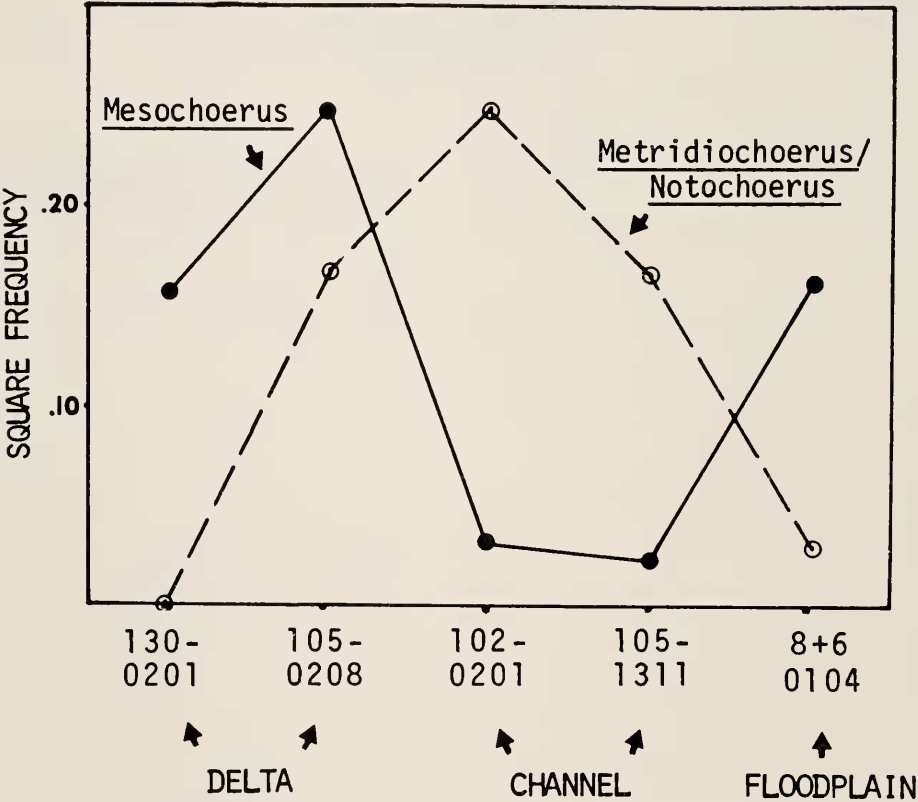


Figure 25. A comparison of the square frequencies of the two suid groups, *Mesochœrus* and *Notochoerus*/*Metridiochoerus*. *Mesochœrus* is considered here to be a more closed habitat (bush) form due to its relationship to the modern *Hylochoerus* (Giant Forest Hog), and to its low-crowned molars, which appear to be adapted for relatively soft vegetation. *Notochoerus*/*Metridiochoerus* suids are more closely related to the modern *Phacochœrus* (Warthog) and have high-crowned molars adapted for abrasive vegetation. These suids may have been more open habitat (grassland) forms. Localities 103-0256 and 103-0267 are omitted due to the low frequencies of suids identifiable to genus (Table 12).

TABLE 13. GENERALIZED ECOLOGICAL CHARACTERISTICS OF RECENT BOVID GROUPS THAT ARE COMMON IN THE EAST RUDOLF FOSSIL ASSEMBLAGES. (MODIFIED FROM R. ESTES, MS. IN PRESS.)

	Habitat	Water proximity		Food habits	Social habits
		Near	Far		
Tragelaphini	Dense Bush	×	(×)	Browsers	small groups
Reduncinae	Woodlands, Floodplains	×		Grazers	small groups
Alcelaphinae	Open grasslands	(×)	×	Grazers	large herds

sistent with predictions based on tooth morphology and recent analogues. The channel assemblages might be expected to sample the more open-country habitats, particularly if the gallery forests fringing the channels are not very extensive. Deltaic environments, if comparable to the most vegetated areas of the recent Omo Delta, would have more forested habitats. The paleoecologic evidence associates *Mesochoeus* with deltaic, potentially more densely vegetated environments and *Notochoerus*/*Metridiochoerus* with fluvial, mixed- to open-habitat environments.

The third molars of the two suid groups are different in size, and there is a possibility that the smaller *Mesochoeus* teeth have been sorted out of the channel deposits. *Mesochoeus* third molars are between about 40 and 60 mm long and 20 mm in height, while *Notochoerus*/*Metridiochoerus* third molars are from about 50 to 75 mm in length and 40 to 60 mm in height. However, the hydraulic equivalents of the teeth in both channels fall within the 10–25 mm range, which is near the median for the total range of other teeth in the deposits as well as the associated sediment. One cannot logically assume that sorting would separate the pig teeth but nothing else with similar size differences. Therefore, sorting can be eliminated, and ecological factors provide the best explanation for the separation of the two suids in the fossil assemblages.

EQUIDS

Although the equid sample is poor and consists mainly of teeth (Figure 24) there

is some suggestion of habitat separation of *Equus* and *Hipparion* in the samples. *Equus* is most abundant in 105–1311 and 102–0201, and *Hipparion* in 130–0201 and 105–0208. There is a time separation between these two groups of samples, but *Equus* is known to occur elsewhere in East Rudolf at the same level as *Hipparion*. The correlation of *Equus* with the channel environments and *Hipparion* with lake margins is comparable to the pattern of occurrences of *Notochoerus*/*Metridiochoerus* and *Mesochoeus*. *Hipparion* is preserved in association with the environment most likely to have been densely vegetated, and *Equus* is found in the deposits more likely to have sampled open country, savanna forms.

BOVIDS

Three bovid groups are abundant enough in the sample assemblages for detailed analysis. These include the Alcelaphinae (hartebeest, etc.), Tragelaphini (kudu, elands, etc.) and Reduncinae (bush buck, waterbuck, etc.). Recent members of these groups are well known in terms of habitat preference (Bigalke, 1972; Estes, in press; Dorst and Dandelot, 1970). Ecological characters are listed in Table 13. Frequencies of bovid tribes in the fossil assemblages are given in Table 14.

All localities combined, alcelaphines and reduncines are nearly equal in abundance, while Tragelaphines are less common. The high frequencies of the smaller alcelaphines in 103–0256 and of both large and small in 105–1311 are significantly larger than the frequencies of the other groups in these localities, with $p \leq .05$ (Chi-square tests).

TABLE 14. FREQUENCIES OF FOSSIL BOVIDS AND THE SMALL HIPPOPOTAMUS IN THE EAST RUDOLF ASSEMBLAGES.

	Delta				Channel		Floodplain
	130-0201	105-0208	103-0267	103-0256	102-0201	105-1311	8+6-0104
Tragelaphini	.24	.10	.20	.00	.12	.16	.02
Reduncinae	.24	.25	.15	.11	.15	.12	.15
Alcelaphinae (<i>Damaliscus</i> -size)	.14	.15	.05	.33	.06	.40	.12
Alcelaphinae (<i>Megalotragus</i>)	.00	.00	.15	.04	.00	.48	.03
<i>Hippopotamus</i> sp. nov.	.05	.20	.10	.26	.09	.00	.06

Reduncines and tragelaphines are of similar frequency except in 103-0256 and 8+6-0104, which have a high proportion of reduncines and few tragelaphines. These differences are probably related to ecological factors since it is difficult to imagine any other processes which could preferentially sort the tribes. (They are of approximately equal body size.) All are represented by multiple skeletal parts where they are abundant. The patterns of occurrence are not as well defined as for the suids, but bush forms (reduncines) are generally more common in the deltaic environments while alcelaphines are associated with the potentially more open environments sampled in the 105-1311 channel and in the 103-0256 mudflats.

The alcelaphine *Megalotragus* is a large, extinct form known only from teeth in the sample assemblages. It has an unusually high frequency in the 105-1311 channel. This is significantly different from its occurrences in the other localities and cannot be explained except by ecological factors. *Megalotragus* is associated with the grassland suids and equid, and may well have been an open-country form itself. Its absence in 102-0201 is somewhat puzzling, if it is typically preserved in fluvial deposits. However, another large bovid (probably *Pelorovis*) is represented in 102-0201 with a frequency of .18. The data may indicate a rather finely resolved habitat separation

between the two forms which can only be clarified by additional sampling.

HIPPOS

The habitat of the extinct small hippo, *H. sp. nov.*, can be generally inferred from its frequency in the bone assemblages (Table 15). It occurs in all localities except 105-1311 and is most abundant in 103-0256. Nearly all the hippo remains in 103-0256 belong to this form, and a variety of skeletal parts exist in the sample squares together with teeth. It is generally more abundant in the deltaic environments, including 103-0267, and is associated with both bush and open country animals. It is definitely autochthonous in the deltaic mudflats environment of 103-0256. From this evidence, it can be concluded that *H. sp. nov.* was probably a lake margin form, preferring deltaic flats with mixed bush and grassland environments. It may have been less aquatic than the larger hippos, but this can only be validly inferred from morphological data, not from the taphonomic evidence now available.

A large extinct hippo, peculiar to the East Rudolf Plio-Pleistocene, cannot be definitely identified in the fossil assemblages from the squares. Ecological data on this hippo would be interesting since somehow three or more forms of *Hippopotamus* managed to coexist at East Rudolf.

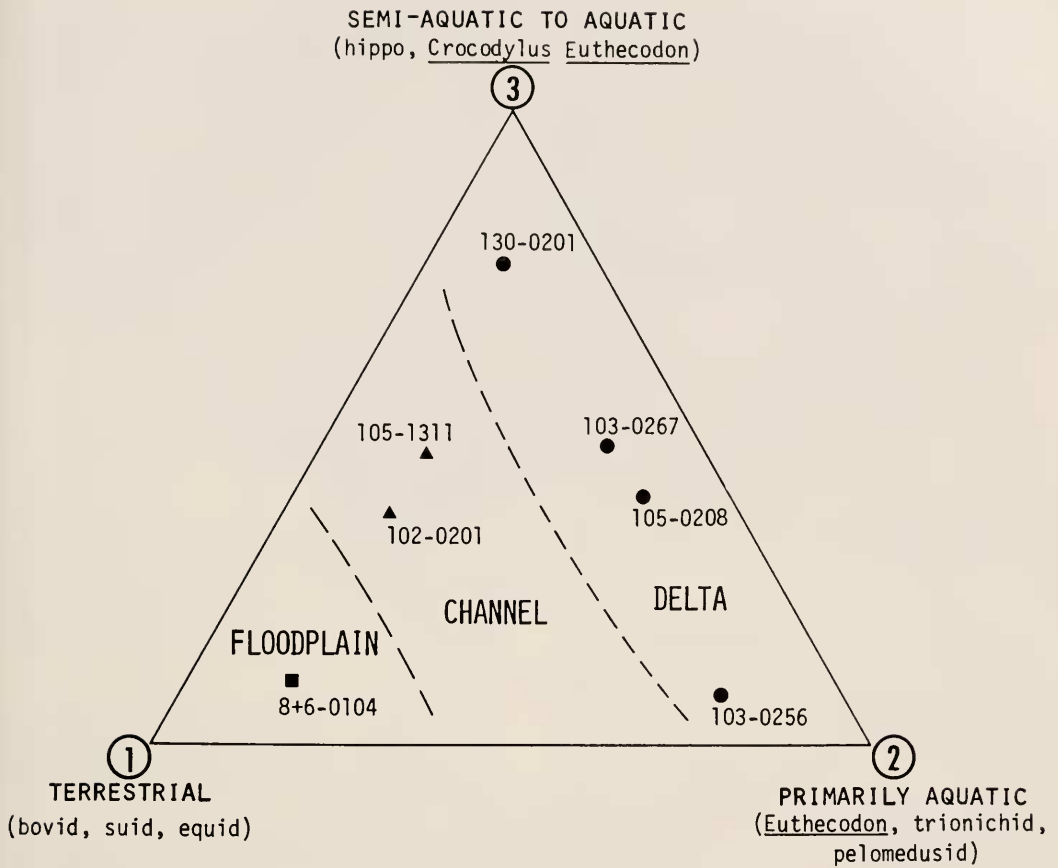


Figure 26. Triangle diagram showing the results of a three factor analysis of the frequency data from all groups of mammals and reptiles. The deltaic localities are spread between two "aquatic" factors, and the channel and floodplain localities are distributed closer to the "terrestrial" factor.

At least one of these is not present in the entire Omo sequence, suggesting significant ecological differences between the two regions, at least as far as the hippos were concerned. We might assume that these differences were expressed in the utilization of broadly different environments. If so, further careful sampling of the sedimentary evidence should reveal more about the ecology of the different hippos.

Conclusions Regarding the Faunal Assemblages

Much of the information provided by the faunal frequencies is summarized in the

triangular diagram in Figure 26. This shows the results of a CAFEAC Q-Mode Factor analysis for three varimax axes (which explains 97% of the variance). The data consist of the square frequencies for all the animal groups given in Table 11. The three factors can be directly related to the aquatic or nonaquatic affinities of the various animals. Factor 1 includes the terrestrial forms and the other two factors include aquatic and semiaquatic forms with affinities for channel or deltaic-lacustrine habitats. These separate the sample localities into three groups depending on their components of aquatic animals.

Thus, the evidence at various taxonomic

levels indicates faunal differences between the localities which agree with environmental interpretations based on geological data. These are real and meaningful *ecological* differences between environments; differences expressed in the square frequencies of the faunas and supported by the geologic and taphonomic characters of the sediments and their bone components. The important points brought out by the faunal data include:

1) The relative numbers of the different vertebrate classes in the fossil assemblages is more dependent on their original numbers and proximity of habitat to a sedimentary environment, than on their aquatic or nonaquatic habits.

2) Relative numbers of animals can indicate whether they were aquatic or nonaquatic in *nonaquatic* sedimentary environments, but not in aquatic ones.

3) The more terrestrial sedimentary environments preserve a greater *diversity* of terrestrial animals. However, the more aquatic environments may preserve an equivalent or greater number of *bones* from terrestrial animals, representing fewer groups.

4) For terrestrial families larger than a baboon or a small antelope, the frequencies expressed in the sample assemblages should be roughly proportional to their original numbers.

5) The more abundant mammals (bovids and hippos) are generally represented by more kinds of skeletal parts of different sorting potential, indicating autochthonous accumulations of bones. This is consistent with the generally autochthonous nature of the assemblages on the deltaic and floodplain environments.

6) The different sedimentary environments clearly preserve different ratios of some animals with different habitat preferences. Terrestrial animals which prefer grassland habitats are found in greater abundance in fluvial deposits, while bush or forest mammals occur in greater abundance in the deltaic deposits. This indicates deltas with denser vegetation than the gallery forests which fringed the channels while the sample bones were accumulating.

PALEOECOLOGY OF THE VERTEBRATE ASSEMBLAGES OF THE KOOBI FORA FORMATION

Much independent but cross-supporting evidence provides a basis for interpreting the paleoecology of the East Rudolf fossil assemblages. These lines of evidence include:

1) *Geologic evidence*. Characteristics of the overall sedimentary environments and the processes operating within them (Fig. 27).

2) *Taphonomic evidence*. a) The extent and type of sorting in the bone assemblages, interpreted with the aid of theoretical considerations from experimental evidence for bone disposal. b) Relationships of the hydraulic equivalences of the bones and of the associated matrix sediment. c) Characteristics of the bone fragments, interpreted according to observations on weathering, fracturing and abrasion of modern bones.

3) *Faunal evidence*. Interpretations based on the faunal composition of the fossil assemblages, using the ecology of modern analogues to Plio-Pleistocene animals.

Figure 27. Block diagrams showing reconstructions of East Rudolf sedimentary environments. Circles show the interpretation of the general sedimentary environment of each fossil sampling locality, indicated by locality numbers. The representation is schematic; the localities do *not* occur on the same time planes or closely adjacent to each other as might be construed from the diagrams. 102-0201 is more closely associated with an emergent delta than can be shown on the diagram. 103-0267 includes a more extensive complex of distributary mouth and beach environments than is indicated by the encircled area.

8+6-0104

FLUVIAL SYSTEM

105-1311

102-0201

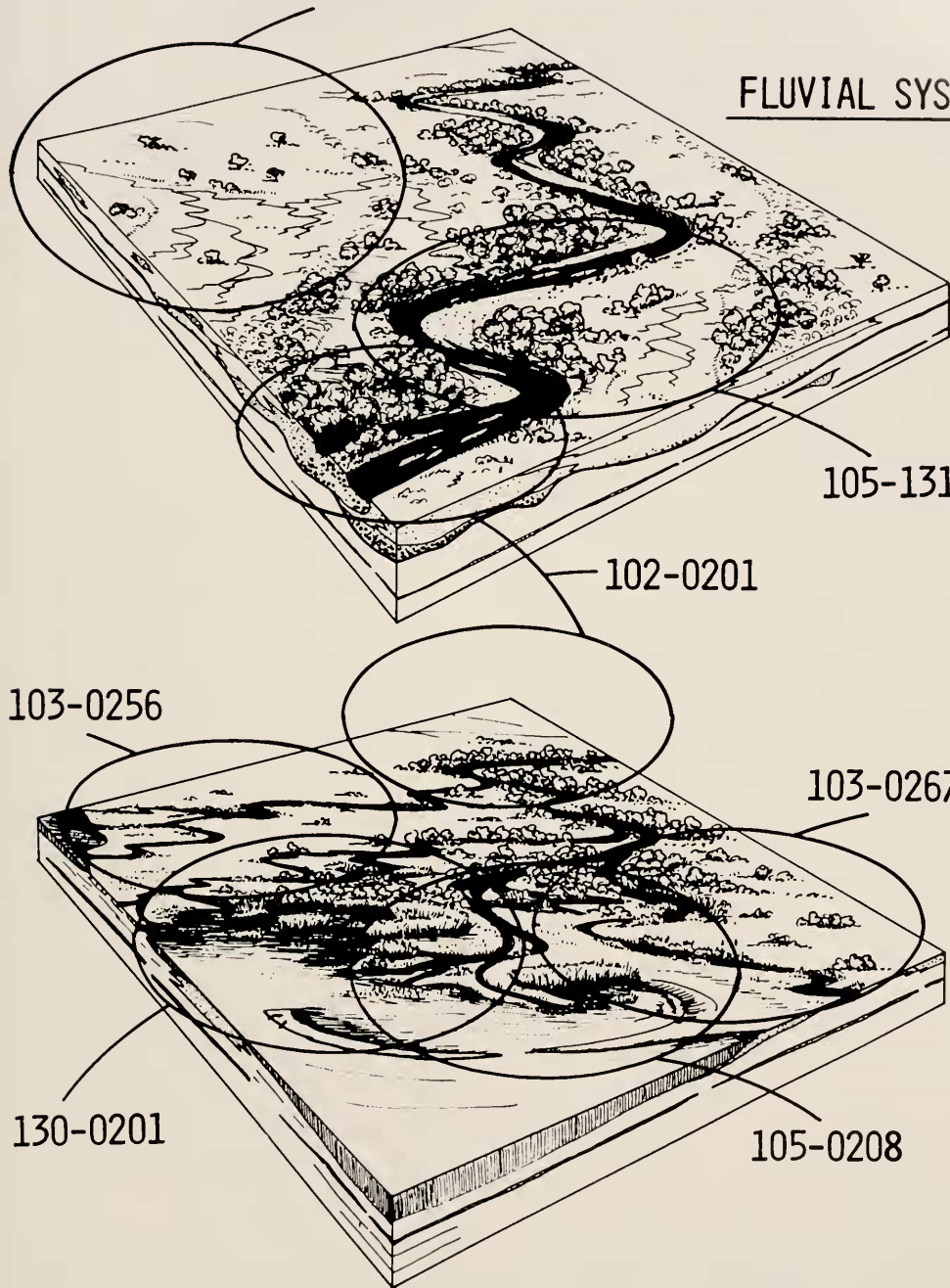
103-0256

103-0267

130-0201

105-0208

DELTA



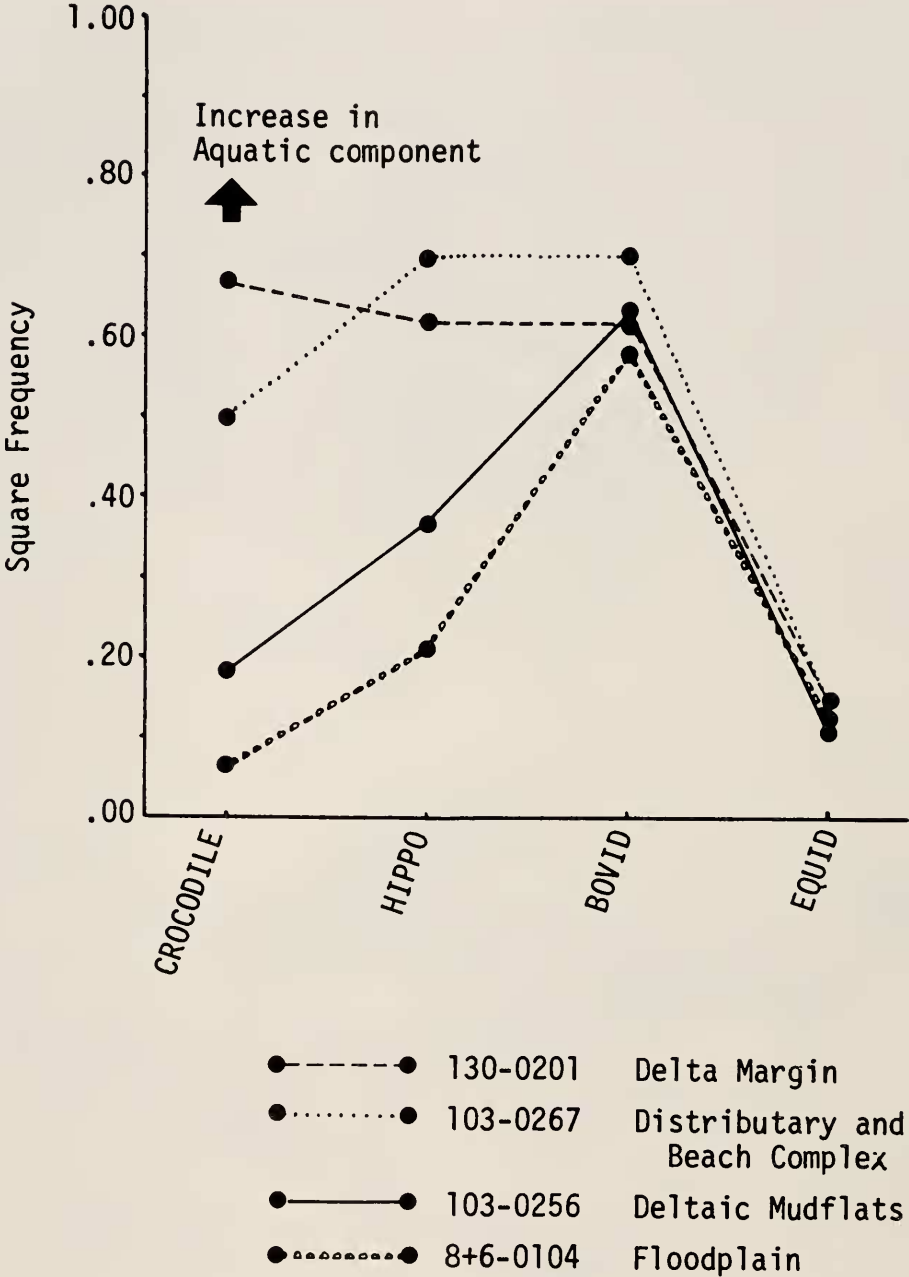


Figure 28. A comparison of the square frequencies of four vertebrate groups with aquatic, semiaquatic and terrestrial habits in four different depositional environments. These environments range from primarily aquatic to primarily terrestrial in terms of their *geologic* characteristics. The frequencies of the aquatic and semiaquatic animals increase as the depositional environments become more aquatic (floodplain to delta margin). However, the frequencies of terrestrial forms remain essentially constant in all environments.

Other lines of evidence can be important in paleoecologic interpretations but are not at present available for the East Rudolf assemblages. These include botanical and geochemical data, which can reveal important factors about vegetation, climate, and salinity of the lake. Continuing research should eventually provide such data.

Ecological Comparisons of the Samples

The overall similarities and differences among localities show that sedimentary environments can be characterized according to distinct taphocoenoses and biocoenoses. At East Rudolf, three broadly defined sedimentary environments are represented: delta, channel and floodplain. The faunas are all basically autochthonous in each of these environments and reveal meaningful ecological differences among them.

AQUATIC AND TERRESTRIAL FAUNAS

The more aquatic sedimentary environments as determined from geologic evidence have an increased representation of aquatic animals but show *no* decrease in the absolute number of terrestrial animals. This is demonstrated in Figure 28 by the increase in the frequencies of crocodilians and hippos relative to bovids and equids. The absolute frequency of bovids and equids does not change significantly from environment to environment, even though these range from floodplain to delta margin.

The pattern of aquatic and terrestrial occurrences can be represented for faunas from each locality as shown in Figure 29. The ratio of terrestrial animals increases as environments become more terrestrial, at the expense of the aquatic forms. The ratio of the semiaquatic hippo, which spends approximately half its time in and half out of the water (Dorst and Dandelot, 1970: 172), changes little from aquatic to non-aquatic environments. These patterns are the result of geologic and taphonomic processes which should have similar effects

on fossil assemblages other than these East Rudolf examples. The crucial variables appear to be: 1) the total volume of bones available from aquatic and nonaquatic animals and 2) the proximity of an animal's habitat to an actively aggrading sedimentary environment. The habits of a fossil vertebrate cannot be inferred from its abundance in an aquatic sedimentary environment unless this can be compared with more terrestrial environments from about the same time.

OPEN AND CLOSED HABITAT MAMMALIAN FAUNAS

The mammalian assemblages provide evidence for two terrestrial faunas with preferences for open (grassland) or closed (bush) habitats. In order to establish these ecological differences, the habitats of the fossil mammals must be inferred from morphologic evidence plus analogy to related living forms. For the paleoecologic interpretation of the East Rudolf fossil assemblages, *Mesochoerus*, reduncines and tragelaphines are used to represent the closed habitat fauna, and *Damaliscus*-size alcelaphines, *Notochoerus*/*Metridiochoerus* suids and *Equus* represent the open habitat fauna. The evidence for relating these mammals to the different ecologic situations has been discussed previously. The ecological separation of such groups according to habitat preference for grassland or bush environments is a common feature of recent East African ecosystems (Lamprey, 1963; Harris, 1970; Estes, 1973).

The relative percentages of closed and open habitat forms in the seven fossil localities are shown in Figure 30. All localities include both, but the deltaic environments in general include more closed habitat forms and the channels more open habitat forms. The deltaic mudflats (103-0256) have an open habitat fauna, in agreement with geologic evidence for an extensive, unforested delta margin environment. The patterns of faunal occurrence indicate that the deltaic, channel and flood-

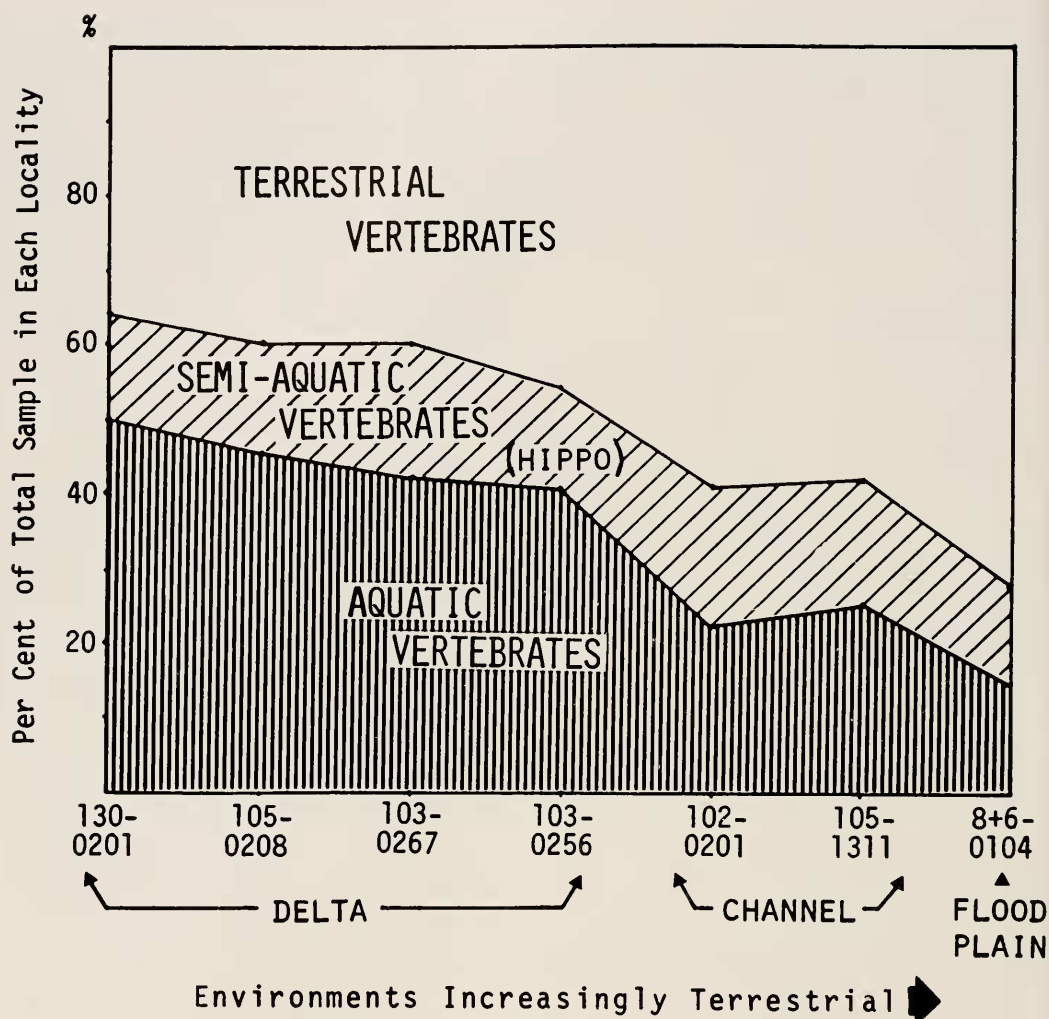


Figure 29. The ratios of aquatic, semiaquatic and terrestrial vertebrate groups represented in the East Rudolf fossil assemblages. The sample localities are arranged from the more aquatic to least aquatic depositional environments on the basis of geologic interpretations. Aquatic animals include crocodilians and chelonians except *Geochelone*; semiaquatic includes only hippopotamus, and all other groups are considered to be terrestrial. Abundance is calculated as the % of the cumulative square frequencies for each locality.

plain sedimentary environments sample both closed and open habitats, but that closed habitats were more abundant on the deltas. A comparison between 130-0201, representing a deltaic fauna, and 105-1311, representing a nondeltaic fauna, shows the most distinct ecological difference among any of the localities (Fig. 31).

COMPARISONS OF KOOBI FORA FORMATION FAUNAS AND RECENT TERRESTRIAL FAUNAS

Bovids, suids and equids are the most abundant large mammals in the fossil assemblages and also in most of the recent undisturbed East African ecosystems (e.g., Foster, 1967; Sheppe and Osborn, 1971). The ratios of these mammals in the fossil

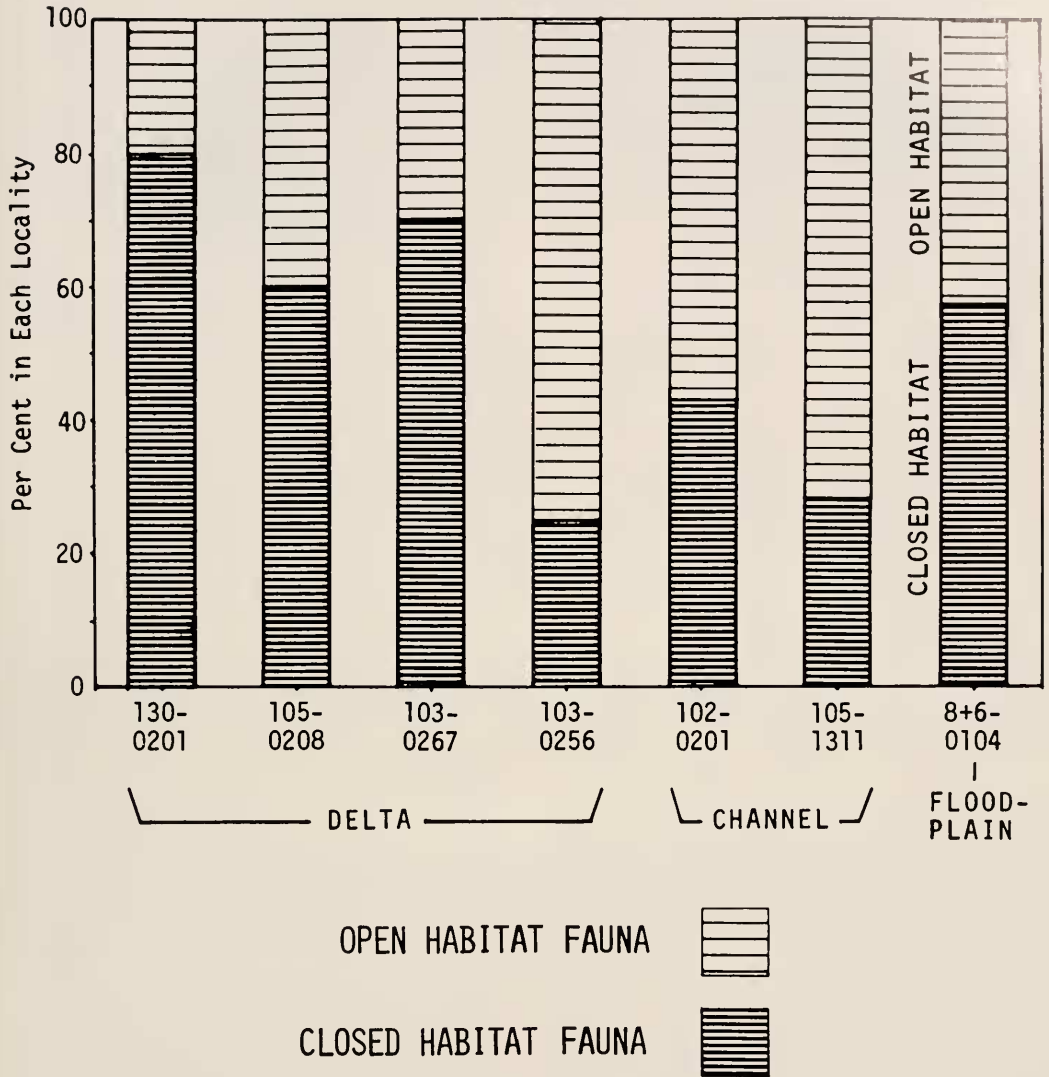
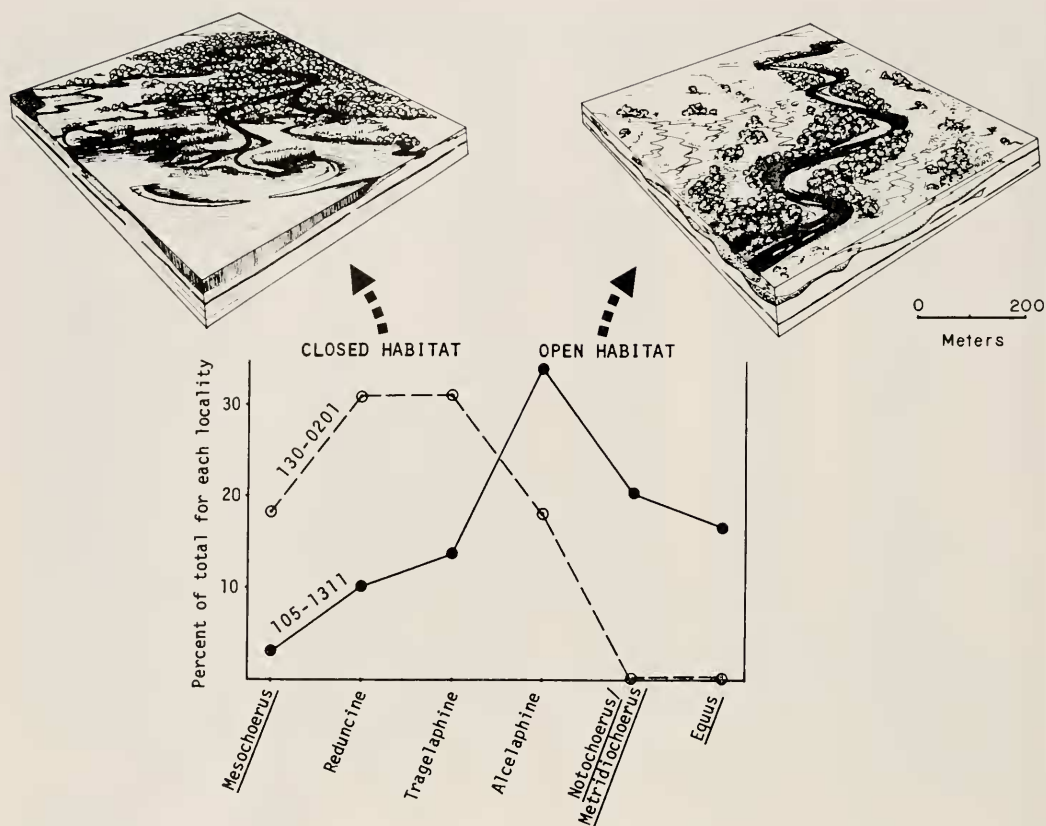


Figure 30. Histogram showing the relative percentages of closed and open habitat mammals in each of the sample localities. Closed habitat forms include *Mesochoerus*, reduncines and tragelaphines; open habitat forms include *Damaliscus*-size alcelaphines, *Notochoerus*/*Metridiochoerus* and *Equus*. Percentages were calculated on the basis of the total square frequencies for the closed and open habitat groups.

faunas is compared with their relative numbers in recent faunas in Figure 32. Bovids are most common in both cases. However, equids are less common than suids in all seven of the fossil sampling localities, and the faunal proportions are most similar to the recent Kafue Park fauna in Zambia. Taphonomic causes do not

adequately explain the greater frequency of suids in the fossil assemblages. Therefore, equids may have lower representation than suids because they were more ecologically separated from the sedimentary environments, or because they were generally less abundant in the East Rudolf region during the time period represented by the



Figures 31. A comparison of the relative abundances of the six mammal groups chosen to represent open and closed habitat faunas in the two localities that show the clearest separation of these two faunas, 105-1311 and 130-0201. Percentages were calculated on the basis of the cumulative totals of square frequencies of the six animals in each locality. The reconstructions represent the *general* sedimentary contexts of each fossil assemblage.

fossil deposits. A greater number of fossil suids agrees well with the greater diversity of this group in the Plio-Pleistocene, with at least 5 species (Maglio, 1972) present in the East Rudolf area.

At present East Rudolf supports a mammalian fauna of at least six bovid species, two species of zebra and a single species of suid, the warthog. Giraffe, hippo, baboon, man and a variety of carnivores and rodents are also present. Rhinoceros has only recently become extinct in the area, and elephants were recorded there near the end of the last century (R. E. Leakey, personal communication). Most

of the fossil mammalian groups are represented in the recent ecosystem, with the exception of the deinotheres, now extinct. However, in terms of species and genera, East Rudolf today is much less diverse than in the Plio-Pleistocene. The fossil faunas are more similar in terms of numbers of species represented (Maglio, 1972) to the recent faunas of wetter areas such as Nairobi National Park or the Kafue Floodplain in Zambia. Environmental change in the East Rodolf region during at least the past 1.5 my. has been great, and apparently is continuing to affect the vertebrate community.

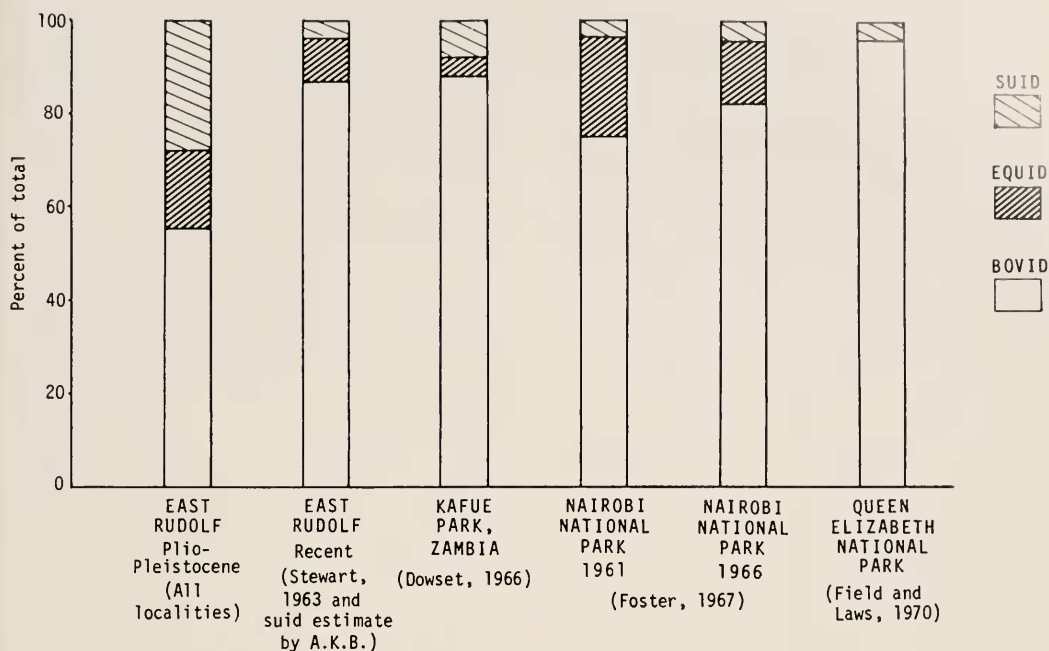


Figure 32. Comparisons of the relative percentages of bovids, suids and equids in the seven Plio-Pleistocene localities used for this study, and in Recent ecosystems. All relative numbers for the recent examples are based on numbers of individuals (game counts). The abundances shown for East Rudolf (Plio-Pleistocene) were averaged from the square frequencies for bovids, suids and equids in all of the seven localities, but are consistent with relative abundances in each separate locality.

Hominid Paleoecology

The hominid fossils that occur in the Koobi Fora Fm. should reflect the same taphonomic processes as the remains of other vertebrates. Therefore, they can be examined in the context of the rest of the fauna for possible paleoecological factors. The abundance of hominids in the East Rudolf collections is due to the intensive program of hominid collecting and does not reflect their relative abundance in the total fauna. In reality, they are fairly rare, as indicated by an occurrence in only 2 out of 213 sample squares in the seven localities used for this study. This is comparable to the relative abundance of rodent fossils in the squares. It would be necessary to sample hundreds or thousands of squares to provide enough hominid material for valid quantitative comparisons of frequencies in different sedimentary environ-

ments. This is not feasible, but it will be possible to relate the hominid fossils to the different sedimentary environments and to the closed or open habitat faunas using the sedimentary and faunal context of each specimen. Based on the patterns of occurrence of other mammals, it seems possible that the two lineages of hominids recognized from East Rudolf (Leakey, 1973) were associated with the two different habitats.

The East Rudolf hominid collection as of April, 1973, consisted of 50 specimens assigned to *Australopithecus*, 34 assigned to *Homo*, and 10 unassigned (M. Leakey, personal communication). Both taxa are represented by a wide variety of skeletal parts. The greater number of *Australopithecus* specimens is due primarily to a larger number of partial mandibles of this form. This may reflect taphonomic processes (e.g., carnivore activity, surface

weathering) that operated to selectively destroy the less robust *Homo* mandibles. There is no clear pattern as yet indicating occurrences of the two forms in different sedimentary environments.⁴ Both occur in deltaic and floodplain deposits. *Australopithecus* is possibly the only hominid occurring in the 105–1311 channel, where it is relatively common (at least 7 separate specimens). This is interesting in that it correlates with other faunal peculiarities of 105–1311, which has a high proportion of open habitat mammals plus forms (deinotheres, rhinos) that are not present in the deltaic assemblages. However, since a variety of habitats were sampled in 105–1311, it would be premature to draw any conclusions on the habitat preferences of *Australopithecus*.

The sample assemblage from 105–0208 occurs in delta margin deposits several meters below the KBS Tuff (Fig. 17), which is the horizon bearing the oldest known hominid "campsites" (Isaac *et al.*, 1972). The relative abundance of the different vertebrate groups (Fig. 23) is probably broadly representative of the fauna that was extant on the delta margin at the time of the hominid habitation sites. At this time, however, the delta margin had changed in position, probably receding farther to the southwest. The deposits directly associated with the KBS Tuff (which is primarily a channel fill) are fine-grained silty clays, which indicate extensive interdistributary marshes and mudflats that were probably seasonally dry. Such environments do not seem to be conducive to fossil preservation on the recent Omo Delta (Butzer, 1971:103), and fossils are indeed rare in the silty clays associated with the habitation sites. Thus, evidence for the faunal context of the tool-manu-

facturing hominids must come indirectly from the older 105–0208 fauna. This provides at least regional, if not local, evidence for the vertebrate fauna most closely associated with the hominids.

East Rudolf in Relation to Other Studies in Vertebrate Paleoecology

Although vertebrate paleoecology has long been an area of recognized research value, there are relatively few comprehensive studies in print. Those that are available provide useful comparisons for paleoecologic interpretations of the Koobi Fora Fm. and show how this study relates to broader research on the evolution of vertebrate communities and ecosystems through time.

The major studies that have defined terrestrial paleo-communities include Olson (1952, 1958), Shotwell (1955, 1963) and Clark *et al.* (1967). Olson's interpretation of the Permian Vale and Choza Fauna of Texas shows a correlation between environmental change (increasing aridity), as determined from geologic evidence, and significant changes in the vertebrate fauna. A study of the Oligocene Chadron fauna of South Dakota by Clark *et al.* (1967:69–73) reveals two distinct ecological assemblages of mammals, referred to as "savanna" and "aquatic-wet forest" faunas. Environmental changes to cooler, more arid conditions led to restriction and finally to the elimination of the wet-forest fauna during the time span represented by the Chadron Fm. Shotwell's studies of Pliocene faunas of the Juntura Basin of eastern Oregon included pioneer work in quantitative methods for reconstructing ecological associations of animals from quarry samples. Using these methods, the fossil mammals of the Drewsey Fm. are assigned to four paleo-communities: woodland, savanna, open grassland and pond-bank. Change through time shows reduction in the woodland and savanna faunas with the development of the open

⁴ Additional research conducted in 1973 indicates that the *Homo* lineage sample is much more restricted to lake margin deposits than the *Australopithecus* sample, which is abundant in both lake margin and fluvial deposits (Behrensmeyer, *In press*).

grasslands fauna (Shotwell, 1963:19). All of these studies rely on geologic and faunal evidence plus a variety of taphonomic assumptions. The paleoecologic interpretations, particularly those of Shotwell, could be further supported or perhaps altered by more detailed taphonomic analysis.

Olson (1952) developed the concept of a "chronofauna" to describe the nature of the vertebrate fauna of the Texas Permian. A chronofauna is defined as "a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time" (1952:181). According to Olson, the members of a chronofauna may change by such processes as expansion into unoccupied niches or the substitution of one species for another in any given niche, but the vertebrate community is in adaptive equilibrium with the environment and will maintain its structure until environmental change occurs. Clark *et al.* (1967) refer to their aquatic-wet forest and savanna faunas as chronofaunas, and Shotwell's communities might also be considered as chronofaunas. The resolution of evidence for the Cenozoic faunas leads to more refined ecological interpretations and to the consideration of shorter time spans than is possible for the Permian.

In these three studies of vertebrate paleo-communities, the chronofaunas show change due to increasingly arid conditions. This leads to the expansion of grassland mammals in the Cenozoic faunas and a decrease in the diversity of the Permian reptile and amphibian fauna. The absence of evidence for significant morphological change in the vertebrate species during the time span represented by the chronofaunas has been noted by Olson (1952:193) and Clark *et al.* (1967:73). During periods of environmental change, extinction, migration and niche modification apparently were more common patterns of faunal response than rapid morphologic modification.

The fauna of the Koobi Fora Fm records interaction between vertebrate communities and environmental conditions between about 3.0 and 1.5 my. B.P. A comparison between the Plio-Pleistocene fauna and the Recent one shows a restriction of species diversity which is more comparable to the terminal stages of the Permian chronofauna than to the shifts in the Cenozoic paleo-communities of South Dakota or Oregon. The general significance of the faunal change at East Rudolf may reflect either the short- or long-term effects of increasing aridity, but it is clearly an example of how environmental change may affect vertebrate communities.

The evidence now available suggests at least one significant difference between the evolution of East African faunas and the evolution of the Texas Permian, the Juntura Basin Mio-Pliocene and the Chadron Oligocene faunas. Some of the East African species, particularly the elephants and suids, show rapid evolutionary change during their Plio-Pleistocene histories (Cooke and Maglio, 1972). Such change has not been recognized in the other faunas, and it is unlikely that this contrast is an artifact of taxonomy or of inadequate sampling. Documentation and comparison of the histories of vertebrate faunas at different time levels and in different regions should do much more to clarify the patterns of evolutionary response to environmental change.

Further reconstruction of vertebrate communities in the Lake Rudolf Basin will provide a more detailed history of faunal change over the past 5-6 my. The open (grassland) and closed (bush) habitat faunas of East Rudolf probably represent distinct ecological communities that can be documented elsewhere in East Africa and followed through time. The Omo sequence offers an ideal opportunity for comparing vertebrate faunas of a major river-floodplain complex with the lake margin faunas of East Rudolf. Using the combination of geologic, taphonomic and faunal evidence,

it will be possible to compare fossil vertebrate communities throughout East Africa and to reconstruct changes in chronofaunas through much of the latter part of the Cenozoic.

SUMMARY

This study has developed methods for deriving paleoecologic information from fossil assemblages of fragmented vertebrate bones subjected to various geologic processes before burial. These methods have been applied to paleoecologic interpretation of the Plio-Pleistocene bone deposits of East Rudolf, Kenya. The conclusions relate to vertebrate assemblages in general as well as to the assemblages of East Rudolf and the Lake Rudolf Basin in particular.

General Conclusions

TAPHONOMY

1) The amount of fragmented bone buried in any given sedimentary environment will depend on the rate of sedimentation and the amount of bone originally put into that environment. The important factors which control bone input are: a) vertebrate abundance, b) carnivore activity, c) the proximity of bones to depositional environments, d) the rates of surface weathering of bones, and e) the dispersal potential of bones. The composition of the resulting fossil assemblage will also in part depend on diagenetic factors.

2) Carnivore activity will have a major effect on the composition of a thanatocoenose. Intense mammalian carnivore activity results in fewer bones of small animals and increased fragmentation of bones of large animals. The evolution of bone-crushing dentitions in mammals has changed the character of Cenozoic taphocoenoses compared with those of the Mesozoic, when reptilian carnivores lacked the capacity for bone mastication.

3) Bones are disarticulated and acquire characters of surface weathering in months

to years if exposed on a land surface. Hydrodynamic transport will tend to leave features of rounding and abrasion on bones. Therefore, well-preserved bones with fragile parts intact and surfaces unflaked or uncracked record conditions of rapid burial without subsequent re-excavation.

4) Bones vary greatly in density, size and shape and are sensitive to hydrodynamic sorting. Disarticulated thanatocoenoses include bones with a wide range of dispersal potentials. This will result in the formation of *dispersal groups* if the bones are subjected to normal or flood-stage current velocities (10–150+ cm/sec.). The dispersal groups will move at different rates from the point of origin. If bones with a wide range of dispersal potentials are found in sedimentary association, this indicates that the assemblage is not a product of *selective transport sorting* of the original thanatocoenose.

5) Mammal bones immersed in water for 5 minutes have densities from < 1.0 to 2.0, and teeth have densities between 1.7 and 2.3. Reptile and fish bones are between 1.3 to 2.3 density. Bones are generally hydraulically equivalent to quartz particles of smaller nominal diameter. Currents should transport bones together with quartz particles that are roughly equivalent hydraulically. Therefore, sedimentary associations of quartz grains and bones of a much larger hydraulic equivalence (e.g., a hippopotamus skull in a siltstone) may indicate other modes of origin for the bone-sediment association. These include *in situ* death, flotation of carcasses, or predator/scavenger transport of bone.

6) Theoretical considerations indicate that velocities of 80 to 200+ cm/sec. must be achieved near the bottom of a flow in order to move bones of moderate density (~ 1.5) and size (100+ cc). Therefore, most disarticulated, water-logged parts of large vertebrates are unlikely to move far from their point of origin except in special transport situations such as floods in channels.

PALEOECOLOGY

1) Ecological characteristics of fossil vertebrates can be defined using a combination of geologic and taphonomic evidence, independent of ecological interpretations based on vertebrate morphology or the adaptation of living analogues. Such evidence can link habitat preferences with preservation in particular sedimentary environments. This correlation can be inferred solely from the geologic context and the taphonomy of a given bone assemblage. Such evidence can then be combined with morphological and recent-counterpart data to support paleoecologic interpretations.

2) Fragmented bone assemblages can be used with confidence for paleoecologic interpretations if they: a) consist of bones with a wide range of dispersal potentials, b) are not hydraulically equivalent to associated sediment and c) retain fresh, unweathered or unabraded surfaces. Assemblages with these attributes can be interpreted as generally autochthonous to their environment of deposition. Most of the animals represented in such an assemblage were preserved in the general context of their original habitats.

3) Aquatic environments of deposition can preserve variable amounts of bone from aquatic and terrestrial vertebrates, depending on the relative bone input from each ecological group. Bone assemblages of terrestrial and aquatic animals in aquatic deposits (e.g., channel, delta margin) may differ only in the better preservation of the latter, not in their greater abundance.

4) Terrestrial environments of deposition (e.g., floodplains) preserve a high proportion of terrestrial vertebrates along with a few aquatic ones. Semiaquatic vertebrates tend to occur in both terrestrial and aquatic deposits, with better representation in aquatic environments.

5) The bone input from groups of large terrestrial vertebrates into fragmented, autochthonous taphocoenoses should generally reflect their relative numbers in the original ecosystem. The fossil abundances

can be used to approximate relative numbers of different vertebrate groups in a given environment. This provides a basis for reconstructing paleo-communities and comparing them through time.

6) Vertebrate communities at different time horizons or in different regions may differ in their response to broad-scale environmental change in ways that can be detected in paleoecologic studies. These responses include rapid morphological evolution, shifts in the relative numbers of animals suited to particular habitats, and a general decline in species diversity accompanied by the extinction of forms in all the available habitats.

Conclusions for the Vertebrate Assemblages of the Koobi Fora Formation, East Rudolf

1) Fossil-bearing deposits reveal sedimentation and bone preservation in at least three major depositional environments: delta margin, channel and floodplain.

2) The three depositional environments show a basic similarity in their representation of different skeletal parts, with teeth the most abundant component. However, the relative numbers of certain skeletal elements differ in ways that reflect the different processes operating in the three environments. Teeth are relatively more abundant in the channel deposits and in the floodplain, while vertebrae and phalanges are more abundant in the delta margin deposits. This can be related to the concentration of heavy, durable parts in the channels through sorting and reworking of bones, and to the absence of such processes in the delta margin environments. The taphonomic characters of the floodplain assemblage indicate preferential removal of the lighter elements without transport or reworking of the associated heavier bones.

3) The sum of taphonomic and geologic evidence shows that the delta margin and floodplain bone assemblages are autochthonous with respect to the overall sedi-

mentary environment. Channels contain a mixture of allochthonous and autochthonous bones and show the most evidence for taphonomic alteration of the original thanatocoenose.

4) The East Rudolf faunas include aquatic, semiaquatic and terrestrial vertebrates that vary in abundance according to sedimentary environment. Analogies with recent East African ecosystems indicate that the relative fossil abundance of terrestrial mammalian families probably reflects their abundance in the original ecosystem. Bovids, suids and equids are the most common groups in the fossil assemblages and in most recent undisturbed East African faunas.

5) Two terrestrial faunas can be defined for the East Rudolf assemblages, based on ecological analogies between recent and fossil mammals. The open habitat fauna includes alcelaphines, *Metridiochoerus*/*Notochoerus* suids and *Equus*. The closed habitat fauna is characterized by *Mesochorus*, reduncines and tragelaphines. There is overlap of these faunas in all of the sample assemblages. However, delta margin deposits generally preserve a greater proportion of closed habitat forms, and the channels preserve more open habitat forms.

7) The paleoecologic results for East Rudolf show that it is possible to define ecological groups of terrestrial vertebrates from surface samples of fragmental bone assemblages. Similar sampling of fossil assemblages at different time horizons can provide a basis for establishing East African chronofaunas and for reconstructing their interaction with environmental changes through time.

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REFERENCES

- ABEL, O. 1912. *Grundzüge der Palaeobiologie der Wirbeltiere*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung Nägele und Dr. Sproesser. 470 pp.
- ALLEN, J. R. L. 1963. The classification of cross-stratified units, with notes on their origin. *Sedimentol.*, **2**: 93-114.
- . 1965. A review of the origin and characteristics of recent alluvial sediments. *Sedimentol.*, **5**: 89-191.
- . 1970. *Physical Processes of Sedimentation*. London: George Allen and Unwin, Ltd. 248 pp.
- ALLEN, P. 1959. The Wealden environment: Anglo-Paris Basin. *Roy. Soc. London, Phil Trans. (B)*, **242**(692): 283-346.
- ANSELL, W. H. F. 1971. Part 15: Order Artiodactyla. In: Meester, J. and H. W. Setzer, (eds.). *The Mammals of Africa. An Identification Manual*. Washington, D.C: Smithsonian Institution Press.
- ARISTARAIN, L. F. 1962. Caliche deposits of New Mexico. Ph.D. Dissertation. Harvard University, Department of Geological Sciences.
- BAKER, B. H., AND J. WOHLFENBERG. 1971. Structure and evolution of the Kenya Rift Valley. *Nature*, **229**: 538-542.
- BEADLE, L. C. 1932. The waters of some East African lakes in relation to their fauna and flora. *J. Linn. Soc. (Zool.)*, **38**: 135-156.
- BEHRENSMEYER, A. K. 1974. Late Cenozoic sedimentation in the Lake Rudolf Basin, Kenya. *Annals Geol. Soc. Egypt*, **IV**: 287-306.
- . In press. The habitat of Plio-Pleistocene hominids in East Africa; taphonomic and microstratigraphic evidence. In C. Joly (ed.), *African Hominidae of the Plio-Pleistocene: Evidence, Problems and Strategies*. New York: Duckworth, Inc.
- BERGGREN, W. A., AND J. VAN COUVERING. 1973. Late Neogene chronostratigraphy, biostratigraphy, biochronology and paleoclimatology. Woods Hole Oceanogr. Inst. Tech. Rep., WHOI-73-40. 334 pp.
- BERRY, L. G., AND B. MASON. 1959. *Mineralogy*. San Francisco: W. H. Freeman and Co. 630 pp.
- BIGALKE, F. C. 1972. The contemporary mammalian fauna of Africa. In Keast, A., B. Glass, F. C. Erk, (eds.). *Evolution, Mammals and Southern Continents*. Albany, New York: State University of New York Press. 141-194.
- BISHOP, W. W. 1968. The evolution of fossil environments in East Africa. *Trans. Leicester Lit. and Phil Soc.*, **62**: 22-44.
- BOWEN, B. E., AND C. F. VONDRA. 1973. Stratigraphical relationships of the Plio-Pleistocene deposits, East Rudolf, Kenya. *Nature*, **242**: 391-393.
- BRAIN, C. K. 1967a. Bone weathering and the problem of bone pseudo-tools. *S. Afr. J. Sci.*, **63**(3): 97-99.
- . 1967b. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Sci. Pap. Namib Des. Res. Sta.*, No. 32.
- BRETZ, J. H., AND L. HORBERG. 1949. Caliche in southeastern New Mexico., *J. Geol.* **57**: 491-511.
- BIGGS, L. I., D. S. MCCULLOCH, AND F. MOSER. 1962. The hydraulic shape of sand particles. *J. Sediment. Pet.*, **32**(4): 645-656.
- BROCK, A., AND C. ISAAC. 1974. Paleomagnetic stratigraphy and chronology of hominid bearing sediments east of Lake Rudolf, Kenya. *Nature*, **247**: 344-348.
- BUTZER, K. W. 1971a. Recent History of an Ethiopian Delta. *Res. Pap. No. 136*, Dept. Geogr. Chicago: The University of Chicago Press. 184 pp.
- . 1971b. The Lower Omo Basin: geology, fauna and hominids of Plio-Pleistocene formations. *Naturwiss.*, **58**: 7-16.
- BUTZER, K. W., G. L. ISAAC, J. L. RICHARDSON,

- AND C. WASHBOURN-KAMAU. 1972. Radiocarbon dating of East African lake levels. *Science*, **175**(4027): 1069-1076.
- CLARK, J., J. R. BEERBOWER, AND K. K. KIETZKE. 1967. Oligocene sedimentation, stratigraphy and paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana, Geol.*, **5**: 158 pp.
- COOKE, H. B. S., AND V. J. MAGLIO. 1972. Pliocene Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution. In Bishop, W., and J. Miller, (eds.). *Calibration of Hominoid Evolution*. New York: Scottish Academic Press. 303-329.
- COTT, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile Crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. *Trans. Zool. Soc. Lond.*, **29**(4): 211-356.
- CURREY, J. 1970. *Animal Skeletons*. London: Edward Arnold, Publishers.
- DAVIES, D. K., F. C. ETHRIDGE, AND R. R. BERG. 1971. Recognition of barrier environments. *Bull. Am. Assoc. Pet. Geol.*, **55**(4): 550-565.
- DODSON, P. 1971. Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Paleogeogr., Paleoclimatol., Paleoecol.* **10**: 21-74.
- . 1974. The significance of small bones in paleoecological interpretation. *Contrib. to Geol., Univ. of Wyoming, Spec. Pap. No. 2* Laramie, Wyoming: Univ. Wyoming Press.
- DORST, J., AND P. DANDELLOT. 1970. *Larger Mammals of Africa*. London: Collins Press. 287 pp.
- DOWSETT, R. J. 1966. Wet season game populations and biomass in the Ngoma area of the Kafue National Park. The Puku (Occas. Pap. Dept. Game and Fish, Zambia), No. 4: 135-145.
- EFREMOV, J. A. 1940. Taphonomy: A new branch of Paleontology. *Panam. Geol.*, **74**: 81-93.
- . 1953. Taphonomie et annales géologiques. *Ann. du Cent. d'Etud. et de Doc. Paléontol.*, No. 4. 164 pp.
- ESTES, R. D. 1967. Predators and scavengers. *Nat. Hist.*, **75**(2, 3): 20-29, 38-47.
- . (1973), in press. Social organization of the African Bovidae. I.U.C.N., Symposium on Ungulate Behavior and Management.
- FIELD, C. R., AND R. M. LAWS. 1970. The distribution of the larger herbivores in the Queen Elizabeth National Park, Uganda. *J. Appl. Ecol.*, **7**(2): 273-294.
- FITCH, F. J., AND J. A. MILLER. 1970. Radiocarbon age determinations of Lake Rudolf artefact site. *Nature*, **226**(5242): 226-228.
- FOSTER, J. B. 1967. Nairobi National Park Game Census, 1966. *East Afr. Wildl. J.*, **5**: 112-120.
- GUGGISBERG, C. A. W. 1972. *Crocodiles*. Newton Abbot, England: David & Charles, Publishers. 195 pp.
- HARRIS, L. D. 1970. Some structural and functional attributes of a semi-arid East African ecosystem. Ph.D. Dissertation, Michigan State University.
- HARVARD TABLES OF THE CUMULATIVE BINOMIAL PROBABILITY DISTRIBUTION. 1955. Cambridge, Massachusetts: Harvard University Press. 503 pp.
- HAYNES, V. 1968. Radiocarbon: analysis of inorganic carbon of fossil bone and enamel. *Science*, **161**: 687-688.
- DE HEINZELIN, J., F. H. BROWN AND F. C. HOWELL. 1971. Pliocene/Pleistocene formations in the Lower Omo Basin, southern Ethiopia. *Quaternaria*, **13**: 247-268.
- ISAAC, G. L. 1967. Towards the interpretation of occupation debris: some experiments and observations. *The Kroeber Anthropol. Soc. Pap.* **37**: 31-57.
- ISAAC, G. L., R. E. F. LEAKEY AND A. K. BEHRENSMEYER. 1971. Archeological traces of early hominid activities, east of Lake Rudolf, Kenya. *Science*, **173**: 1129-1134.
- JOHNSON, L. C. 1965. Morphological analysis in Pathology. In Frost, H. M. (ed.). *Bone Biodynamics*. (Henry Ford Hospital Int. Symp.). Boston: Little, Brown and Co. 543-654.
- KONIZESKI, R. L. 1957. Paleoeecology of the middle Pliocene Deer Lodge Local Fauna, western Montana. *Bull. Geol. Soc. Am.* **68**: 131-150.
- KRUUK, HANS. 1972. *The Spotted Hyaena*. Chicago: The University of Chicago Press. 335 pp.
- KURTEN, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zool. Fenn.*, **76**: 5-118.
- LAMPREY, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *East Afr. Wildl. J.*, **1**: 63-92.
- LANGBEIN, W. B., AND L. B. LEOPOLD. 1968. River channel bars and dunes—theory of kinematic waves. *U.S. Geol. Surv. Prof. Pap.* No. 422-L: 1-20.
- LEAKEY, R. E. F. 1973. Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1972. *Nature*, **242**: 170-173.
- LEOPOLD, L. B., M. G. WOLMAN AND J. P. MILLER. 1964. *Fluvial Processes in Geomorphology*. San Francisco: W. H. Freeman and Co. 522 pp.

- LEOPOLD, L. B., W. W. EMMETT AND R. M. MYRICK. 1966. Channel and hillslope processes in a semiarid area, New Mexico. U. S. Geol. Surv. Prof. Pap. No. 352-G: 193-253.
- LOBOVA, E. V. 1967. Soils of the Desert Zone of the USSR. Jerusalem: Israel Program for Scientific Translations. 405 pp.
- LOVERIDGE, A. 1941. Revision of the African terrapin of the family Pelomedusidae. Bull. Mus. Comp. Zool., **88**(6): 462-524.
- LOVERIDGE, A., AND E. E. WILLIAMS. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool., **115**(6): 163-557.
- MAGLIO, V. J. 1972. Vertebrate faunas and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. Nature, **239**: 379-385.
- McKEE, E. D., E. J. CROSBY AND H. L. BERRYHILL, JR. 1967. Flood deposits, Bijou Creek, Colorado, June, 1965. J. Sediment. Pet., **37**(3): 829-851.
- MILLAR, C. E., L. M. TURK AND H. D. FOTH. 1966. Fundamentals of Soil Science. New York: John Wiley & Sons. 491 pp.
- MULLER, A. H. 1957. Lehrbuch der Palaozoologie. Vol. 1: Allgemeine Grundlagen. Jena: Gustav Fischer Verlag. 322 pp.
- OLSON, E. C. 1952. The evolution of a Permian vertebrate chrono-fauna. Evolution, **6**(2): 181-196.
- . 1958. Fauna of the Vale and Chosa: 14. Fieldiana, Geol., **10**(32): 397-448.
- PATTERSON, B., A. K. BEHRENSMEYER, AND W. D. SILL. 1970. Geology and fauna of a new Pliocene locality in north-western Kenya. Nature, **212**(5062): 918-921.
- PAYNE, J. E. 1965. Summer carrion study of the baby pig, *Sus scrofa*. Ecology, **46**(5): 592-602.
- PETTJOHN, F. J. 1957. Sedimentary Rocks. New York: Harper & Row, Publishers. 718 pp.
- PETTJOHN, F. J., P. E. POTTER AND R. SIEVER. 1972. Sand and Sandstone. New York: Springer-Verlag. 618 pp.
- REEVES, C. C. 1970. Origin, classification and geologic history of caliche on the southern high plains, Texas and eastern New Mexico. J. Geol., **78**: 352-362.
- REIF, WOLF-ERNST. 1971. Zur Genese des Muschelkalk-Keuper-Grenzbonebeds in Südwestdeutschland. Neues Jahrb. Geol. Palaontol. Abh., **139**(3): 369-404.
- RITTENHOUSE, G. 1943. Transportation and deposition of heavy minerals. Bull. Geol. Soc. Am., **54**(12): 1725-1780.
- SADEK-KOOROS, H. 1966. Jaguar Cave: an early man site in the Beaverhead Mountains of Idaho. Ph.D. Dissertation. Harvard University, Department of Anthropology.
- SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. Am. Nat., **102**(925): 243-282.
- SCHÄFER, W. 1972. Ecology and Palaeoecology of Marine Environments. Craig, G. (ed.), I. Oertel (transl.). Chicago: The University of Chicago Press. 568 pp.
- SCHALLER, G. B. 1972. The Serengeti Lion. Chicago: The University of Chicago Press. 480 pp.
- SELOUS, F. C. 1908. African Nature Notes and Reminiscences. London: MacMillan and Co. 356 pp.
- SHAPIRO, A. H. 1961. Shape and Flow: The Fluid Dynamics of Drag. New York: Doubleday & Co., Inc., Anchor Books. 186 pp.
- SHEPPE, W., AND T. OSBORNE. 1971. Patterns of use of a floodplain by Zambian mammals. Ecol. Monogr., **41**(3): 181-205.
- SHOTWELL, J. A. 1955. An approach to the paleoecology of mammals. Ecology, **36**(2): 327-337.
- . 1963. The Juntura Basin: studies in earth history and paleoecology. Trans. Am. Phil. Soc., (N.S.), **53**(1): 3-77.
- SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative Zoology. New York: Harcourt, Brace & World, Inc. 440 pp.
- STEWART, D. R. M. 1963. Wildlife census, Lake Rudolf. East Afr. Wildl. J., **1**: 121.
- VAN LAWICK-GOODALL, H. AND J. 1971. Innocent Killers. Boston: Houghton Mifflin Co. 222 pp.
- VISHER, G. S. 1965. Use of vertical profile in environmental reconstruction. Bull. Am. Assoc. Pet. Geol., **49**(1): 41-61.
- VOORHIES, M. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contrib. to Geol. Univ. of Wyoming. Spec. Pap. No. 2. Laramie, Wyoming: Univ. Wyoming Press. 69 pp.
- WALSH, J. AND R. G. DODSON. 1969. Geology of Northern Turkana. Rep. No. 82, Geol. Surv. Kenya. 42 pp.
- WEIGELT, J. 1927. Rezente Wirbeltierleichen und ihre paläobiologische Bedeutung. Leipzig: Verlag von Max Weg. 208 pp.
- WHITE, T. 1955. Observations on the butchering techniques of some aboriginal peoples, numbers 7, 8, and 9. Am. Antiq., **21**(2): 170-178.
- WILLIAMS, G. E. 1971. Flood deposits of the sand-bed ephemeral streams of Central Australia. Sedimentology, **17**: 1-40.

APPENDIX 1

MEASUREMENTS OF DENSITIES, VOLUMES AND WET WEIGHTS OF MODERN BONES. DENSITIES ARE CALCULATED FOR THE BONES AFTER THEIR PORE SPACES WERE FILLED WITH WATER.

DENSITIES

Skeletal part	<i>Ovis</i> (sheep) MCZ 1939	<i>Redunca</i> (reedbuck) MCZ 14917	<i>Hylochoerus</i> (forest hog) MCZ 27851	<i>Damaliscus</i> (topi) MCZ 15724	<i>Equus</i> (zebra) MCZ 5003	<i>Hippopotamus</i> MCZ 5020
HUMERUS	1.53	1.40	1.55	1.51	1.77	1.74
RADIUS }		1.58		1.72		
ULNA }	1.64	1.16	1.66	1.41	1.45	1.69
FEMUR	1.45	1.36	1.41	1.37	1.36	1.79
TIBIA	1.46	1.23	1.54	1.71	1.45	1.55
METATARSAL	1.44	1.33	1.07	1.62	1.68	1.50
METACARPAL	1.35	1.45	1.15	1.51	1.52	1.34
ASTRAGALUS	1.68	1.81	1.28	1.66	1.16	1.46
CALCANEUM	1.62	1.37	1.22	1.50	1.00	1.52
PODIAL #1	1.43	1.13	1.30	1.46	1.23	1.31
#2	—	1.25	1.20	1.48	1.01	1.46
PHALANX #1	1.45	1.34	—	1.40	1.00	1.37
#2	1.60	—	1.36 ⁽¹⁾	1.34	1.02	1.29 ⁽¹⁾
#3	1.06	—	1.02 ⁽¹⁾	1.01 ⁽¹⁾	1.05 ⁽¹⁾	1.07 ⁽¹⁾
TEETH M	2.19	—	—	2.23	2.08	2.00
PM	—	—	—	2.24	1.97	1.97
C	—	—	1.53	—	—	1.83
I	—	—	1.53	1.88	—	1.74
RIB #1	1.11	1.54	1.41	1.36	1.22	1.63
#2	—	1.43	1.20	1.08	1.84	—
VERTEBRA ATLAS	1.24	.78	1.56	1.43	1.28	1.64
AXIS	1.07	.94	1.41	1.33	1.24	1.87
CERVICAL	1.04	1.13	—	1.11	.98	1.82
THORACIC	1.06	1.05	1.21	1.30	1.11	1.26
LUMBAR	.89	1.23	1.23	1.13	.99	1.36
SACRUM	1.11	.92	1.18	1.07	—	—
PATELLA	1.07	1.07	1.01	1.30	.64	1.24
PELVIS	1.19	1.17	—	—	—	—
STERNUM	.97	—	—	—	—	—
SKULL	1.42	1.39	—	—	—	—
JAW (½)	1.43	1.74	—	1.58	—	—
SCAPULA	1.65	1.88	—	1.53	—	—
VERT. CENT. #1	.98	.75	1.60	1.00	1.06	1.29
#2	1.09	—	1.40	—	1.00	—
ULNA, PROX.	—	.90	—	1.21	—	—
SESAMOID #1	—	—	—	—	—	1.46
#2	—	—	—	—	—	1.18
HUM. PROX.	1.26	1.34	1.42	1.32	1.63	1.55
DIST.	1.75	1.96	1.69	1.81	1.83	1.96
R. U. PROX.	1.64	1.47 ^(R)	1.65	1.96 ^(R)	1.29	1.74
DIST.	1.59	1.72 ^(R)	1.67	1.52 ^(R)	1.50	1.63
FEM. PROX.	1.47	1.44	1.50	1.58	1.33	1.83
DIST.	1.42	1.30	1.29	1.21	1.45	1.64
TIB. PROX.	1.32	1.20	1.27	1.43	1.27	1.30
DIST.	1.64	1.28	1.96	2.30	1.77	1.91
MT. PROX.	1.31	—	—	1.48	1.49	—
DIST.	1.56	—	—	1.55	1.36	—
MC. PROX.	1.38	—	—	1.33	1.40	—
DIST.	1.25	—	—	1.37	1.40	—
SCAPULA (GLENOID)	1.30	1.48	1.58	1.29	1.32	—

R = Radius only.

t = Terminal Phalanx

VOLUMES (Cubic Centimeters)

Skeletal part	<i>Ovis</i> (sheep) MCZ 1939	<i>Redunca</i> (reedbuck) MCZ 14917	<i>Hylochoerus</i> (forest hog) MCZ 27851	<i>Damaliscus</i> (topi) MCZ 15724	<i>Equus</i> (zebra) MCZ 5003	<i>Hippo- potamus</i> MCZ 5020
HUMERUS	53.5	67.0	404	225	310	2542
RADIUS }		39.0		148		
ULNA }	39.6	11.0	232	39.0	303	1700
FEMUR	65.0	116	383	296	635	3000
TIBIA	56.0	128	186	246	411	1852
METATARSAL	21.0	46.0	23.0	117	140	144
METACARPAL	20.5	40.0	25.5	116	176	174
ASTRAGALUS	4.1	7.2	27.5	20.4	63	296
CALCANEUM	5.5	14.1	44.5	36.0	87	352
PODIAL #1	2.8	6.4	12.2	16.2	10.4	150
#2	—	2.0	8.8	5.6	14.8	94
PHALANX #1	2.9	4.5	12.0	17.9	48	78
#2	1.0	4.8	7.4 ⁽¹⁾	8.1	—	17.8 ⁽¹⁾
#3	1.7	—	8.5 ⁽¹⁾	7.9 ⁽¹⁾	20.0 ⁽¹⁾	10.7 ⁽¹⁾
TEETH M	1.7	—	—	3.6	25.4	73.0
PM	—	—	—	—	—	17.6
C	—	—	42.2	—	—	290
I	—	—	—	0.8	—	130
RIB #1	10.0	5.2	55.0	14.0	26.5	229
#2	—	7.7	31.8	33.0	25.0	—
VERTEBRA ATLAS	25.0	24.4	75.0	63.0	139	866
AXIS	30.5	19.8	56.0	67.0	155	500
CERVICAL	24.0	18.4	—	62.0	170	450
THORACIC	14.0	8.4	57.0	22.8	64.0	480
LUMBAR	15.6	16.6	45.0	40.0	49.0	480
SACRUM	30.0	33.0	165	125	—	—
PATELLA	2.9	5.2	28.0	20.0	45.0	244
PELVIS	107	64.0	—	—	—	—
STERNUM	3.2	—	—	—	—	—
SKULL	209	124	—	—	—	—
JAW (½)	39.5	23.0	—	119	—	—
SCAPULA	26.0	20.5	—	110	—	—
VERT. CENT. #1	5.1	6.0	25.0	20.0	31.0	233
#2	4.7	—	25.0	30.0	28.0	—
ULNA, PROX.	—	7.8	—	20.0	—	—
SESAMOID #1	—	—	—	—	—	7.0
#2	—	—	—	—	—	10.6
HUM. PROX.	32.5	35.0	220	129	168	1420
DIST.	23.4	24.0	184	94.0	150	1122
R/U. PROX.	19.5	21.0 ^(R)	117	65.0 ^(R)	170	822
DIST.	20.1	18.0 ^(R)	115	84.0 ^(R)	147	878
FEM. PROX.	32.0	55.0	179	128	325	1466
DIST.	33.0	61.0	204	168	299	1634
TIB. PROX.	31.0	66.0	113	154	235	1100
DIST.	25.0	62.0	73.0	96.0	168	750
MT. PROX.	11.5	—	—	61.0	68.0	—
DIST.	9.7	—	—	58.0	68.0	—
MC. PROX.	10.0	—	—	60.0	82.0	—
DIST.	12.0	—	—	58.0	90.0	—
SCAPULA (GLENOID)	16.6	13.0	97.0	65.0	100	—

WET WEIGHTS (Grams)

Skeletal part	<i>Ovis</i> (sheep) MCZ 1939	<i>Redunca</i> (reedbuck) MCZ 14917	<i>Hylochoerus</i> (forest hog) MCZ 27851	<i>Damaliscus</i> (topi) MCZ 15724	<i>Equus</i> (zebra) MCZ 5003	<i>Hippo- potamus</i> MCZ 5020
HUMERUS	82.1	93.5	626	340	550	4413
RADIUS }		61.6		255		
ULNA }	64.9	12.8	385	55	440	2869
FEMUR	94.5	158	539	407	866	5364
TIBIA	82.1	158	286	420	597	2873
METATARSAL	30.3	70.8	24.7	190	244	216
METACARPAL	27.7	62.3	29.3	171	176	234
ASTRAGALUS	6.9	13.2	35.1	33.9	71	432
CALCANEUM	8.9	19.9	54.3	54.0	88	536
PODIAL #1	4.0	7.2	15.8	23.7	12.8	196
#2	—	2.5	10.6	8.3	15.0	137
PHALANX #1	4.2	6.3	—	21.9	49	107
#2	1.6	7.1	12.2 ^(†)	11.4	47	23 ^(†)
#3	1.8	—	10.2 ^(†)	7.5 ^(†)	21 ^(†)	11.5 ^(†)
TEETH M	4.4	—	—	6.7	68.7	146
PM	—	—	—	11.4	M35.0*	35
C	—	—	64.5	—	—	530
I	—	—	—	1.5	—	226
RIB #1	11.1	8.0	77.8	18.7	34.2	374
#2	—	11.0	38.2	35.8	46.0	—
VERTEBRA ATLAS	30.9	19.0	117	90.0	178	1418
AXIS	32.6	18.7	78.7	89.0	193	934
CERVICAL	24.9	20.7	—	69.0	166	818
THORACIC	14.8	8.8	69.2	29.7	71.3	606
LUMBAR	13.9	20.4	55.3	45.0	48.9	652
SACRUM	33.4	30.5	195	134	—	—
PATELLA	3.1	5.9	28.4	25.9	29.0	276
PELVIS	127	75.0	—	—	—	—
STERNUM	3.1	—	—	—	—	—
SKULL	296	171	—	—	—	—
JAW (½)	56.5	40.0	—	—	—	—
SCAPULA	43.0	38.6	—	168	—	—
VERT. CENT. #1	5.0	4.5	40	25.0	33.0	300
#2	5.1	—	35	—	28.0	—
ULNA, PROX.	—	6.4	—	30.0	—	—
SESAMOID #1	—	—	—	—	—	10.2
#2	—	—	—	—	—	12.5
HUM. PROX.	41.0	47.0	313	170	275	2206
DIST.	41.0	47.0	313	170	275	2206
R/U. PROX.	32.0	31.0 ^(R)	192	127 ^(R)	220	1434
DIST.	32.0	31.0 ^(R)	192	127 ^(R)	220	1434
FEM. PROX.	47.0	79.0	269	203	433	2682
DIST.	47.0	79.0	269	203	433	2682
TIB. PROX.	41.0	79.0	143	220	298	1436
DIST.	41.0	79.0	143	220	298	1436
MT. PROX.	15.1	—	—	90.0	88.0	—
DIST.	15.1	—	—	90.0	88.0	—
MC. PROX.	13.8	—	—	85.0	122.0	—
DIST.	13.8	—	—	85.0	122.0	—
SCAPULA (GLENOID)	21.5	19.3	153	84.0	132.0	—

* M = Molar.

APPENDIX 2

Calculation of Hydraulic Equivalence

Processes of sediment transport are generally explained in terms of quartz grains with a standard density of 2.65. Some work has been done on the hydraulic equivalence ("equivalent settling velocity") of quartz and particles with greater densities to show how small, dense grains sort out with larger, lighter ones (Rittenhouse, 1943; Briggs, 1962). However, there is a lack of information on the hydraulic equivalence of quartz with particles of lower density such as bones.

Hydraulic equivalence can be considered in terms of any two particles that have the same settling velocity. Given a particular bone, it is possible to determine what size of quartz grain will settle at the same rate as the bone. For spheres, hydraulic equivalence to quartz can be easily calculated using the Impact law. If the settling velocity for quartz (v_q) is to equal the settling velocity of a bone (v_b), then:

$$1307 \cdot (\rho_q - 1) \cdot r_q = 1307 \cdot (\rho_b - 1) \cdot r_b$$

$$(\rho_q - 1) \cdot r_q = (\rho_b - 1) \cdot r_b$$

$$1.65 \cdot r_q = (\rho_b - 1) \cdot r_b$$

$$r_q = \frac{(\rho_b - 1) \cdot r_b}{1.65}$$

$$\rho_q = 2.65$$

$$\rho_b = \text{bone density}$$

$$r_q = \text{radius of quartz grain}$$

$$r_b = \frac{1}{2} \text{ the nominal diameter of a given bone.}$$

If $\rho_b = 1.5$ and $r_b = 1.0$ cm, then $r_q = .30$ cm.

The value of r_q represents an idealized quartz equivalent for the bone which disregards the effects of shape.

It is difficult to predict the effects of shape on bone-quartz equivalents. In some cases bone shape may decrease settling velocity by increasing the frictional drag on the bone, and this will reduce the size of the equivalent quartz grain. On the other hand, a bone shape (e.g., a streamlined one) that reduces drag may increase the size of the quartz equivalent. The orientation of a bone may have great effects on settling velocity and quartz equivalence. Thus, a metapodial dropped parallel to its long axis may fall faster than a sphere of equivalent volume, but the same bone dropped with its long axis horizontal could settle at a rate slower than that of a sphere. The same bone can alter from equivalence to small or large quartz grains by slight changes in orientation. In actual transport situations, some bones tend to orient with long axes parallel to current direction (Voorhies, 1969:66-67), and these will have maximum hydraulic equivalents for their volume. Bones also tend to orient perpendicular to the current, and these will have smaller effective quartz equivalents. The bones that orient transverse to the current should be more mobile in transport situations.

There is a great need for experimental work which will show the relationship between bone settling velocities and quartz equivalents and the actual current velocities necessary for bone entrainment and transport.

Plate 1. Surface textures of weathered and unweathered bones.

- A: a) Unweathered recent bovid radius, showing a smooth, "fresh" surface texture; b) Naturally weathered bovid femur from the recent East Rudolf thanatocoenose, showing slight roughening and cracking of the bone surface; c) Distal end of an equid femur from the recent East Rudolf thanatocoenose, showing extreme flaking and roughening of the bone surface. (Scale in 1 cm and 2 cm intervals)
- B: a) Fossil astragalus from the 102-0201 channel sand, showing pre-burial abrasion; b) Fossil astragalus from the 103-0267 distributary channel and beach complex, showing considerable pre-burial abrasion; c) Recently weathered astragalus from the modern East Rudolf thanatocoenose, showing the typical cracked weathering pattern on its articular surface (Note: pattern lacking in a) and b)); d) Recent, unweathered astragalus; e) Unweathered and unabraded fossil astragalus from Locality 8+6-0104 (floodplain). (Scale in 1 cm and 2 cm intervals)
- C: a) Distal end of a fossil humerus that was probably weathered prior to burial, showing the typical cracking pattern on its articular surface; b) Distal end of a recently weathered humerus, showing a similar cracking pattern; c) Recent, unweathered humerus; d) Fossil humerus from Area 8, East Rudolf, showing no sign of pre-burial weathering or abrasion. (Scale in 1 cm and 2 cm intervals)

Plate 2. Fracture patterns in recent and fossil bones.

- A: a) "Sawtooth" fracture (right side of bovid pelvis); b) "Step" fracture (bovid metapodial); c) "Splintered" fracture (sheep rib); d) "Spiral" fracture (distal end of bovid humerus; e) Weathered bovid humerus (distal end) with a spiral fracture incurred prior to weathering. (Scale in 1 cm intervals)
- B: Spiral fracture on the metatarsal of a recently killed giraffe, presumably caused by a hyaena. (Scale in 10 cm intervals)
- C: a) and b) Typical fracture patterns of bones after mineralization; c) Recent humerus (distal) showing spiral fracture; d) Fossil fragment of a diaphysis, showing a spiral fracture probably incurred prior to burial and mineralization. (Scale in 1 cm and 2 cm intervals)

Plate 3. The trapping effect of surface vegetation on bones in the recent thanatocoenose on the delta of Laga Tulu Bor, Ileret, East Rudolf.

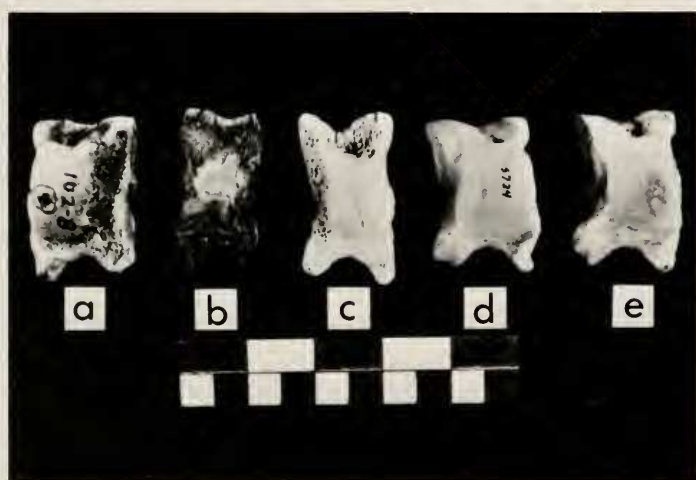
- A: Bovid femur bound by shoreline grass and partially buried. (Scale in 10 cm intervals)
- B: Bovid skull and vertebrae, showing loose entrapment by grass. The horn cores are bound firmly to the ground by warm tubes (just to right of camera lens cover).

Plate 4. Recent sedimentary environments south of Ileret, East Rudolf.

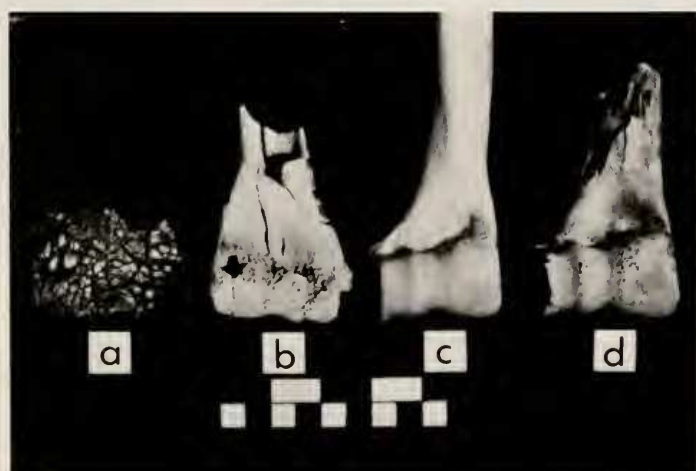
- A: A beach bar on the shore of the delta of Laga Tulu Bor, with the open lake to the right and a closed lagoon or back beach pond to the left. Pebbles and bone debris litter the beach. Beach bars such as this move shoreward seasonally with the annual rise in lake level (about 1 m fluctuation per year). Depositional environments such as this were probably active in the formation of Plio-Pleistocene deposits such as those of Localities 130-0201, 105-0208, 103-0267 and 103-0256.
- B: Laga Tulu Bor after a brief but heavy rainstorm, with a flow depth of about 1.5 m. The channel is normally dry for most of the year. A break in the gallery forest that fringes the channel is visible in the upper right of the photograph. This opens onto the grass-covered floodplain. Some characteristics of this depositional environment are probably comparable to Localities 102-0201 and 105-1311.
- C: The upper part of the deltaic plain of Laga Tulu Bor, showing flooding of a low area (atrophied channel) after a heavy rain. This area lies in the transition zone between floodplain and deltaic plain. The sediment is primarily silt. This depositional environment is probably comparable to that of Locality 8+6-0104 (floodplain).



A

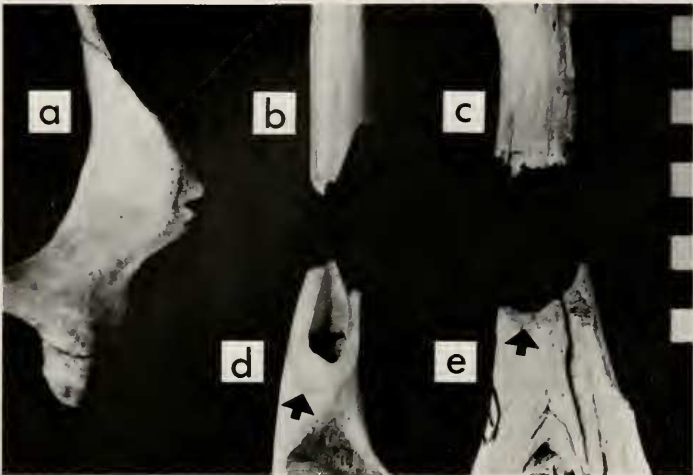


B



C

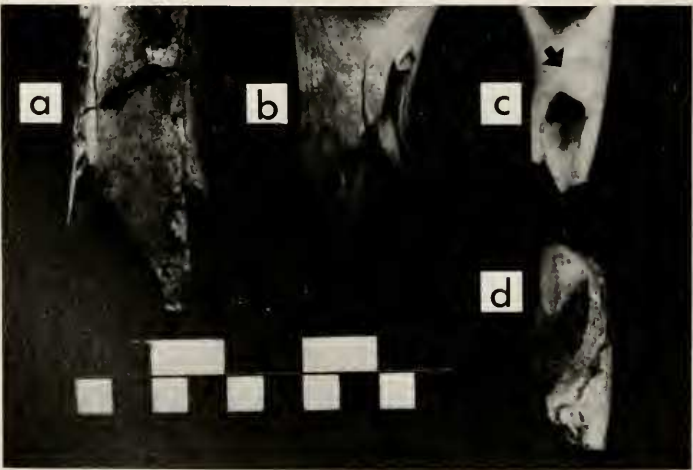
Plate 1



A



B



C

Plate 2

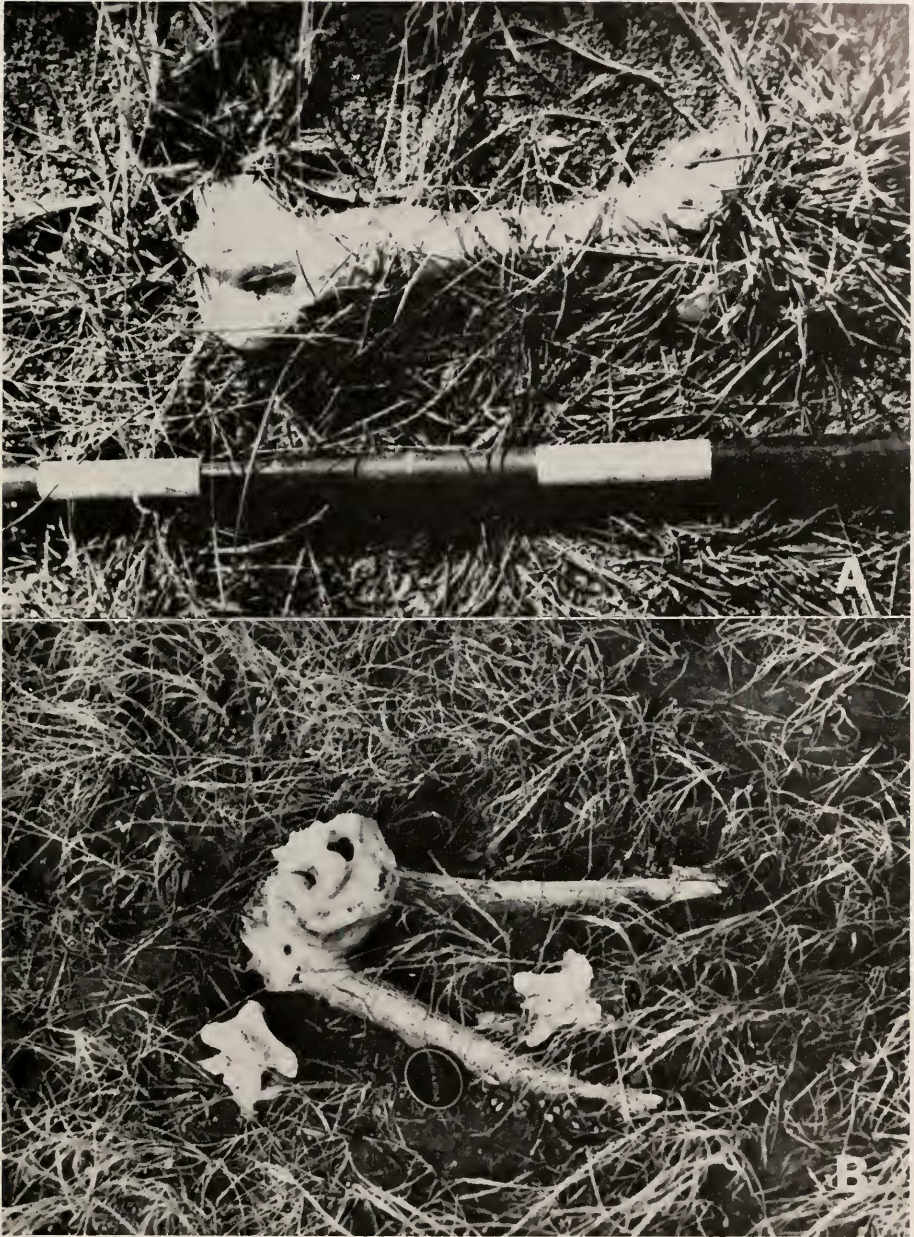


Plate 3

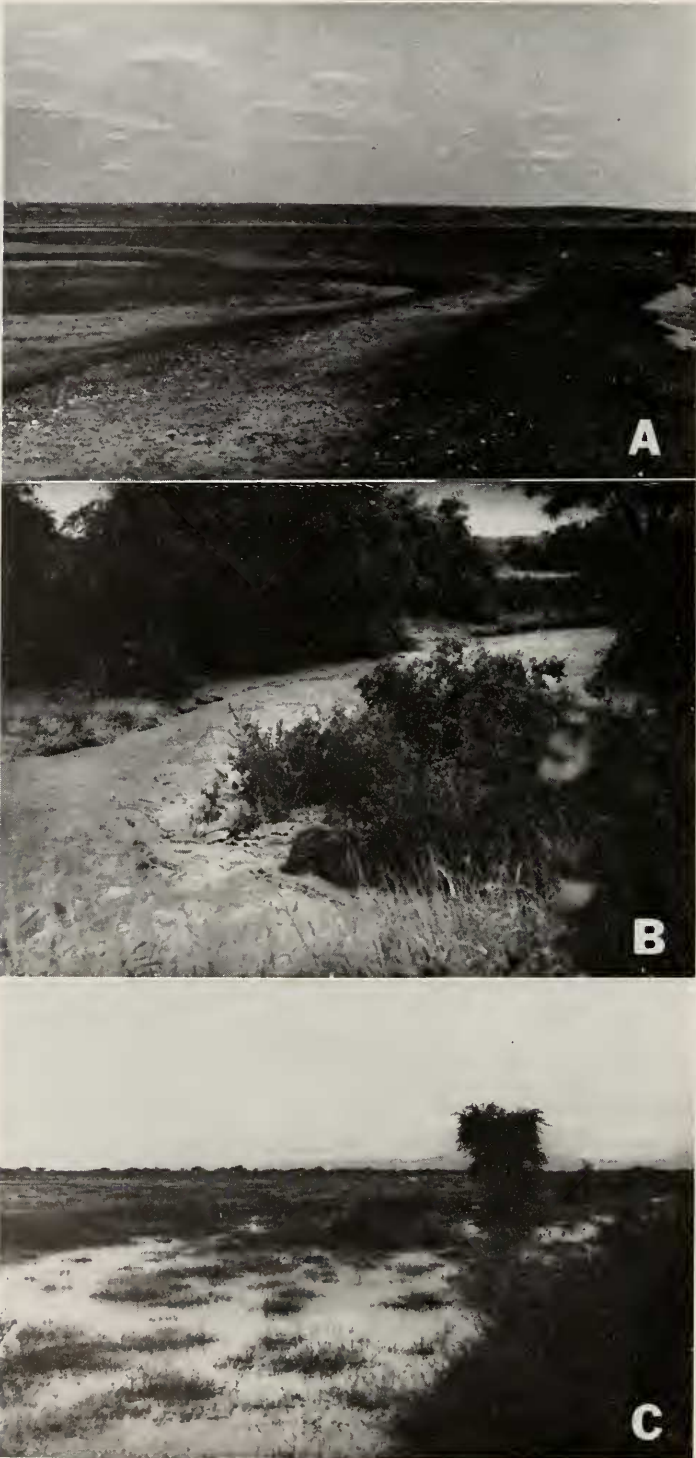


Plate 4

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